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VOLUME 31 JANUARY, 1957 NUMBER 1

UPPER ALBIAN (CRETACEOUS) AMMONOIDEA FROM TEXAS

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ABSTRACT—This paper brings part of the classification of upper Albian ammonites up to date and up to modern standards for some of the Texas species. Twelve new species are described (*Drakeoceras georgetownense, D. drakei, D. arringtoni, D. kummeli, D. gabrielense, D. dellense, D. lasswitzi, Durnovarites adkinsi, Deiradoceras amsburyi, Pervinquieria whitneyi, P. smedalae, Prohysteroceras, P. atchisoni*) and two previously described species are redescribed. The fourteen species are distributed through six genera, two of which are new (*Drakeoceras* and *Craginites*); all six genera are classified as Mortoniceratinae (Ammonitina).

INTRODUCTION

MORE refined biostratigraphic studies in the Cretaceous rocks of Texas require the description of many additional species and the completion of more up to date taxonomy for the Gulf Coast ammonites, particularly those of the Lower Cretaceous. Since the papers by Böse (1928) and Adkins (1928, 1929, 1931, 1933), those by Kummel & Decker (1954), Jones (1938), Renz (1936), and Stephenson (1954) are the only ones on the Upper Cretaceous which cover ammonite species pertaining specifically to areas in Texas. Although various workers in Mexico (Humphrey [1949], Imlay [1938, 1940], and others) have aided in the description of Neocomian, Aptian and lower Albian species, some of which may be found in Texas, only Albritton (1937), for the Neocomian, and Scott (1941), for the Upper Aptian and lower Albian, have done any systematic work on Lower Cretaceous ammonites in the Texas area within the last 20 years.

The present paper consists of descriptions of new species from the Upper Albian, and represents only a partial coverage of species representative of the subfamily Mortoniceratinae. Of course the scheme of taxonomy followed by many authors dealing with Cretaceous ammonites, whose works were not directed specifically toward Texas, has a direct bearing on the nomenclature and taxonomy of Texas species. Foremost among these works, which pertain to the present study, are those of Spath (1922, 1923, 1933, and others). Important also are the works of Wright (1952, 1955), Haas (1942), and Van Hoepen (1931, 1941, 1942, 1944, 1946a, 1946b, 1951a, 1951b). On subjective grounds only the taxonomy of Haas (1942) and Van Hoepen (1944 and others) must remain suspect, Haas for being too conservative, Van Hoepen for being insufficiently conservative. In the writer's opinion, the criticism of Van Hoepen by Spath (1933, 1934), and more openly by Haas (1942), was not altogether justified, at least not on the grounds presented by Haas. The writer might prefer to remain out of this argument, but the uncertainty concerning some of this South African material is producing taxonomic problems

which are very pertinent to the present study, and which may not be cleared up until a disinterested person restudies the South African collections. Spath (1922) and Haas (1942) both regretted the lack of detailed stratigraphic knowledge concerning their respective collections; Spath's (1922) fauna undoubtedly contains elements of the *dispar* zone, and Spath believed that all of the species were representative of the upper Albian. Haas (1942) likewise took pains to indicate the distribution of his species, but, without definite information, indicated that the conclusions were tentative. Yet both of these authors condemned Van Hoepen (1931, 1941) for his new genera, superficially resembling forms of theirs, but of middle Albian age, and apparently of different lineage.

This predicament has resulted in the writer proposing a new genus in the present paper, which could perhaps be united with one of the Angola stocks (as yet unnamed generically) were we less ignorant of ammonite lineages and ages. Furthermore, the writer believes that less confusion has been caused by naming new genera than by the incorrect application of otherwise valid genera [e.g., the application of *Acanthoceras* to certain horned forms of the basal Cenomanian (Scott, 1926, and others) which almost 30 years ago caused the suspicious and able Emil Böse (1928) to use the term "vicariating" when speaking of these forms of the basal Cenomanian which "recurred" in the upper Cenomanian].

Although certain relationships are suggested in the present paper, no lineages, as such, are proposed. Lineages are not proposed because the status of description is too incomplete. The mere fact that each worker can propose lineages in his part of the world which are completely unacceptable in some other area is in itself an indication of the extremely small sample of species that has so far been described.

I can propose lineages that are reasonable for Texas species, but which not only do not agree with Van Hoepen's (1944), even when his phylogenies are interpreted in my generic terms, but which are completely unacceptable in South Africa. The same lineages will likewise be as unacceptable to European workers as are Van Hoepen's. This probably means one of two things, either there are generic and subgeneric provinces more sharply delineated than heretofore supposed (which might not be surprising if more were known of the distribution of modern cephalopod genera) or the number of species described so inadequately represents the supply that the true picture is still obscured. In any event far less than one-half of the Lower Cretaceous ammonite species of Texas have been named and described.

Taxonomic criteria.—Much has been written concerning the value of different characters for classificatory purposes. Each worker has and will continue to have his own pet characters which, no matter how objective he attempts to be, will prejudice him. I have neglected the suture pattern, largely because the present forms are so preserved as to yield only incomplete and meager sutures for illustrations. In addition a catalogue of well over a thousand sutures, diagrammed, stylized, and natural, has failed to yield criteria valid below the family level except for a few unusual genera. In my opinion, authors who designate genera and/or species on sutures only are daydreaming.

Whorl sections are extremely informative, but useful only between comparable ontogenetic stages (e.g., the sections in Text-fig. 1–h are all taken from the last volution of an uncrushed internal mold. Unless this were known they might not be assumed to be from the same species).

Spath, Haas, and Van Hoepen are about the only specialists on Cretaceous cephalopod who have consistently given costal sections, and of these only Van Hoepen in sufficient numbers. Haas almost alone illustrates costal and intercostal sections together, but in insufficient number. The lack of costal and intercostal sections has hindered the comparison of different groups from different areas. The preservation of the Texas material is such as to prevent the use of old mouth edges and apertural features, all of which can be extremely important.

A good many years ago Adkins (1928) divided *Pervinquieria* Böhm), as he knew it, into two groups, those with fine inner costation and those with coarse inner costation. Each of these he then divided into two

groups, based on whether or not adult forms were trinodose. Enlarging upon the system then begun by Adkins, a terminology for juvenile costation is used for convenience in classification and description. This classification may have some phylogenetic significance, but experimentation, testing, and checking with other methods of classification and with ideas of other workers will be necessary before any realistic conclusions can be drawn. In the meantime this classification is meant only to be morphologic. The four types of juvenile costation considered in this paper are as follows:

(1) *Goodhallitine*—This type of costation consists of flexiradiate ribbing, weakly or moderately umbilituberculate; ribbing is not coarse, is flexiradiate, and nearly always bifurcates from the umbilical tubercle; it is best exemplified by *Goodhallites goodhalli* var. *tuberculatus* Spath (1934). Some of the costation may be as paucicostate as in the young of *Goodhallites gracillimus* (Kossmat), and in this species appears to be transitional to the mortonicerine type of ribbing described below, but even when paucicostate the goodhalliitine type of costation remains flexiradiate. On the evidence in Texas, it appears to be derived directly from a dipolocerine type, and the mortonicerine type, in turn, may be derived from a coarse goodhallitine type. On the other hand, the Angola evidence, as now understood, would not support such derivations.

(2) *Mortonicerine*—This type of costation is coarse, usually rectiradiate, always bifurcating, always bituberculate, and usually umbilituberculation is nodate; costation and tuberculation are strong. An example is *Mortoniceras leonensis* (Conrad, 1857) although the bifurcation is frequently more pronounced than in this species. This type of costation is typical of the group of *leonensis* of Adkins (1928).

(3) *Pervinquieriine*—This type of costation seems also to be derived directly from a dipolocerine ribbing, described below. It may or may not have a very early bituberculate stage, perhaps usually so; not enough very young shells have been examined to be certain. Most important, there is always a juvenile, faintly trituberculate stage, not present in either mortonicerine or goodhallitine types. This juvenile stage takes on the appearance of the costation in *Pervinquieria kiliani* (Lasswitz), and has long been termed *kiliani*-ribbing. Examples would include *Pervinquieria kiliani* (Lasswitz) and the juvenile stages of *Pervinquieria inflata* (J. Sowerby).

(4) *Dipolocerine*—Although *Dipoloceras* is not a member of the subfamily Mortoniceratinae, some of the genera classified in this subfamily (Wright, 1952) possess juvenile ribbing of the dipolocerine type. This costation is typified by the young of many of the species of *Dipoloceras*, but not all at various stages, and is best exemplified by the ribbing of *Dipoloceras pseudaon* Spath var. *moniliforme* Spath (1931). In this type of costation the ribs are relatively densicostate; they are uneven and there may be one, two, or three grades of ribbing: (1) beginning at the umbilicus with a small bullate tubercle and extending ventrad, (2) beginning at about the end of the first third of the flank and extending ventrad, and (3) beginning at about the end of the second third of the flank and extending ventrad. Bifurcations may be present, but most ribs are single. The only tuberculation beside the very small bullate umbilical tubercle consists of spirally arranged papillae which are usually nodate, but more often absent than present. There may be in addition a very weak, bullate shoulder tubercle. Although the young whorls of *Dipoloceras* Hyatt are inflated, the dipolocerine ribbing may occur in the young of genera in which the juvenile whorls possess flattened flanks.

Such a classification for juvenile ribbing is not always discrete and breaks down between certain taxa. There seems to be a plexus between those forms with juvenile mortonicerine ribbing and those forms with juvenile goodhallitine ribbing in the vicinity of certain species described under the genus *Cainoceras* by Van Hoepen (1942, 1951b) and in "*Schloenbachia*" *gracillima* (Kossmat).

There is also a transition from the genus *Goodhallites* to the genus *Drakoceras*, n. gen., in the lower part of the upper Albian of Texas, but thereafter, in Texas at least, the distinction remains quite sharp.

No definite transition from *Goodhallites* to *Pervinquieria* Böhm is apparent, but this may be by definition of the two genera.

Pervinquieria appears to more likely descend from some such form as *Craginites*, n. gen., or other appropriate group with juvenile dipolocerine ribbing. *Goodhallites* likewise is descended from something similar, and in both the lines of descent form plexi or retes in three dimensions, being polyphyletic in the sense that some of Wright's (1952) family units are polyphyletic.

Terminology.—The terminology employed in this paper is that of Spath (1923) and Adkins (1928). The abbreviations used are H = whorl height; W = whorl width (t = thickness in Adkins); D = diameter of shell; and U = diameter of umbilicus. In order to make comparisons on the inner whorls without destroying specimens I have employed another measurement called HF. HF is the direct linear distance from the umbilical suture to the base of the keel. It is not as accurate a measurement as H for descriptive purposes, but many more measurements per individual ammonite may be obtained. Haas (1955) has recently used a similar measurement which he calls H, but he measures to the periphery. The keels are incompletely preserved on most specimens studied by the writer. H′ of Haas is H of the writer.

W is measured intercostally. All measurements except D and HF/W are reported as percentages of D; D is recorded in mm. Under the descriptions of the various species measurements are systematically recorded from left to right in the following manner.

D	U	HF	W	HF/W	Costation T	P	S	B

In the column on costation T is the total number of costae per volution at the designated diameter, P is the number of primary costae (single), S the number of secondary costae (single), and B the number of bifurcating costae, always recorded in pairs (e.g., B = 8 pr). Whorl sections are given at shell diameters in all specimens where such were possible to measure. U is also designated at definite shell diameters.

Occurrence of fossils.—All of the fossils herein described were collected from carbonate rocks, either marls, shaly limestones, or limestones. This does not mean that the same species cannot occur in other rock types. Moreover, all of the fossils herein described were collected from platform sections and from shallow water facies. So far there is no observational data to indicate a preference among non-reef, shallow water carbonate sediment environments. The same fossils may occur with equal abundance in marl, shaly limestone, or limestone. A far greater number of fossils may be collected from marl and shaly limestone than from limestone, but this may be because of easier collecting, the fossils not weathering out of the harder limestone. On the other hand, there is a greater abundance of oysters in the Washita group in those carbonate rocks that weather as marls. The distribution of oysters in turn should have influenced the distribution of other animals. Ammonites are unknown in the Fredericksburg or Washita reef associations.

Craginites, n. gen., has been collected from limestone, shaly limestone, calcareous shale, non-calcareous lutite, and quartz arenite. *Drakeoceras*, n. gen., and *Durnovarites* are known only from calcareous rocks in Texas, but *Pervinquieria* has been collected from a greater variety of lithologies.

All of the fossils except *Craginites* n. sp.,

EXPLANATION OF PLATE 1

Durnovarites adkinsi, n. sp. (p. 6)

FIG. *1,2,7*—Lateral, dorsal, and ventral views, ×1; UT 695, lower *Turrilites brazosensis* zone, Georgetown limestone, 500 feet N of McNeil road on the old road to Georgetown from Austin, Travis Co., Texas.

3,6—Lateral and ventral views of holotype, ×1; UT 10064, lower part of *Turrilites brazosensis* zone, 15 feet below top of Georgetown limestone, Pease Park, Shoal Creek, Austin, Texas; collector: K. Young, 1953.

4,5—Lateral and ventral views, *4*×2, *5*×1; UT 10824, lower part of *Turrilites brazosensis* zone, Georgetown limestone, 1.5 mi. E of Brodies Lane on Oak Dale Drive, in creek bottom, Austin, Travis County.

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n. gen., are internal molds, and most of the internal molds bear one or more of the attached oysters discussed by Hyatt (1903). Usually the nonseptate body chamber, lacking structural support, has been destroyed or broken, but occasionally the lucky collector finds a complete individual, or perhaps a single body chamber. The individuals have suffered the varying degrees of solution common to carbonate rocks, and the sutures are usually poorly preserved.

Acknowledgments.—Although the paleontological conclusions contained herein are those of the writer, many persons are responsible for bringing together material and ideas. Not least among these are a number of geologists who did at least part of their graduate work at the University of Texas. Particularly valuable has been the work of D. E. Atchison (1954), R. T. Arrington (1954), Gerald F. McCarthy (1952), and Billy Walls (1950). In addition the experience and knowledge of W. S. Adkins has been invaluable, and his concepts have no doubt influenced the writer greatly.

Many students in the geology department at the University of Texas have aided in filing and cataloguing fossils.

Dr. J. T. Lonsdale, Director of the Bureau of Economic Geology, The University of Texas, has made the Bureau collections available and some of the collecting was done under mapping projects for that organization. Prof. R. K. DeFord and his students have supplied collections and information from West Texas and Trans Pecos Texas.

SYSTEMATIC PALEONTOLOGY

The repository abbreviations, UT and BEG, indicate, respectively, the Paleontology Collection, Department of Geology, and the Bureau of Economic Geology, both of The University of Texas, Austin.

Class CEPHALOPODA
Order AMMONOIDEA de Haan, 1825
Suborder AMMONITINA Hyatt, 1889
Superfamily ACANTHOCERATACEAE Hyatt, 1900
Family HYSTATOCERATIDAE Hyatt, 1900
Subfamily MORTONICERATINAE Spath,* 1932
Genus DURNOVARITES Spath, 1932
Type species: *Durnovarites subquadratum* Spath, 1932.

Generic characters.—*Durnovarites* Spath is an ammoniticone with U=25–45. The ribs are coarse and bituberculate in early stages (mortonicerine), becoming quadrituberculate in the later neanic stage, and in some forms, becoming more densicostate, before becoming paucicostate on the body chamber. More typical species have an extremely low H/W ratio (H/W=ca. 0.75), less typical forms have a higher H/W ratio, but width is always greater than height. Umbilical, flank and double shoulder tubercles produce the quadrituberculate appearance so characteristic in this genus, and in the type species the ventral element of the shoulder tubercle is almost texanitid.

Observations.—According to Spath (1932, 1942) *Durnovarites* is characteristic of the

* Unlike Wright (1952) I prefer to credit Spath (1932) with the family name. This for the simple reason that Douvillé (1911) did not refer to the present family but to the group now called *Texanites* Spath, which is placed in the Peroniceratidae by Wright (1952). I still think it proper to thus indicate that Spath's usage is being followed rather than the usage of Douvillé.

EXPLANATION OF PLATE 2

FIG. *1*—*Prohysteroceras atchisoni*, n. sp. Lateral view of holotype ×½; UT 10529, zone of *Eopachydiscus brazoense*, 4 feet above the base, bed 8, section 8, loc. 11 of D. E. Atchison (1954); Georgetown limestone, Lake Creek, southwest Round Rock, Williamson Co. Texas; collector: D. E. Atchison. (p. 13)

2,5—*Pervinquieria smedalae*, n. sp. Lateral and ventral views of holotype, ×½; UT 10106, zone of *Drakeoceras maximum*, Georgetown limestone, Berry Creek, ¼ mi. down stream from the U. S. highway 81 bridge, Williamson Co., Texas; collector: R. T. Arrington, 1953. (p. 10)

3,4—*Pervinquieria whitneyi* , n. sp. Ventral views of holotype ×1; UT 10530, zone of *Oxytropidoceras bravoense*, Georgetown limestone, bed 4, section 8, loc. 11 of Atchison (1954), from beneath railroad bridge over Lake Creek, southwest Round Rock, Williamson Co., Texas; collector: D. E. Atchison, 1954. (p. 10)

dispar zone. The Texas species, to be described below, occurs in the youngest Mortoniceratinae-bearing strata in central Texas. The genus appears to be unrelated to *Angolaites* Spath, and the group of *D. perinflatum* (Spath) could be descended from some such a leonitid as *Mortoniceras wintoni* (Adkins), which, with its low H/W ratio, by the addition of a true flank tubercle and reduction of the umbilical tubercle could lead to the group of *D. perinflatum* very easily. However, forms such as *D. postinflatum* Spath, with more robust juvenile ribbing, or the more spinose species such as *D. subquadratum* Spath and especially *D. spinosum* (Pervinquiere) (non *Durnovarites spinosum* Van Hoepen), seem to be more difficult to evolve from such an ancestor. Such larger forms as *D. perinflatum* (Spath), *D. adkinsi*, n. sp., and *D. quadratum* Spath, become more paucicostate on the outer whorl. Most species of *Durnovarites* have yet to have the body chamber described. *Durnovarites* is not related to *Angolaites* Spath (1932), not only because of the difference in general appearance, but because of the juvenile mortonicerine ribbing in *Durnovarites* and juvenile pervinquieriine costation in *Angolaites*. *Drakeoceras*, n. gen., never has a true flank tubercle and has goodhallitine juvenile costation.

DURNOVARITES ADKINSI, n. sp.

Pl. 1, fig. 1–7; Pl. 7, fig. 4; Text-fig. 1g,k,m

Holotype.—UT 10064, from 15 feet below the top of the Goergetown limestone, from the top of the *Drakeoceras drakei* zone, Pease Park, Shoal Creek and 18th Street, Austin, Travis County, Texas.

Specific characters.—Oligogyral, concentrumbilicate, gradumbilicate, widely subangustumbilicate to narrowly sublatumbilicate, carinate; whorl section wider than high (HF/W=0.75 to 0.90), the holotype at a diameter of 82 mm. being widest intercostally between the umbilical tubercle and the flank tubercle and widest costally at the flank tubercle. UT 10864, at a diameter of 18 mm., is widest just dorsad of the ventral tubercle (only two tubercles at this stage). UT 695, at a diameter of 75 mm., is widest at mid flank. The widest part of the shell appears to migrate dorsad with age. Flanks and venter are rounded intercostally, and the keel is low and rounded.

Costation is moderate to paucicostate in the early neanic stage, is dense to a diameter of about 75 mm. where it then becomes less dense, there being 40 more or less ribs per volution at a diameter of 75 mm. and about 28 costae per volution at a diameter of 35 mm. The costae are weakest between the umbilical and flank tubercles. Most ribs are bifurcating at the umbilical tubercle, a few primary and single, and there are scattered intercalations beginning just dorsad of the position of the flank tubercle.

The umbilical tubercle is low and bullate, hanging over the umbilical wall which is at right angles to the overlapped flank. The flank tubercle is slightly bullate. The shoulder tubercle is double, the dorsal element nodate, the ventral element bullate, elongated with the rib allignment, the ribs swinging orad on the venter. At a diameter of 20 mm. this form is bituberculate (costation is mortonicerine). It could not be ascertained how the other two tubercles were derived, but the flank tubercle probably arises independently as a low swelling on the rib at mid flank. The ventral element of the shoulder tubercle would seem to arise later than the dorsal element, developing first as a low swelling on the end of the rib extending as a ventrad tapering of the dorsal element. (This is similar to the development of the double shoulder tubercle in *Mortoniceras*, and the juvenile of this species at a diameter of 20 mm. is very similar to individuals of *Mortoniceras* at the same diameter.).

Overlap is dorsad of the dorsal element of the shoulder tubercle, so that only the umbilical and flank tubercles can be observed on the inner whorls when the outer whorl is in place. On the holotype septation ceases at a diameter of 60 mm., and costation is coarser and less dense on the last ¾ of the last whorl or the body chamber,* and tubercles are larger and more pronounced; the apertural margin is not present on this specimen, but most of the body chamber is present. UT 10824 is septate through 88

* Most textbooks call this the living chamber, which is certainly a misnomer in fossils. I prefer body chamber which parallels nicely the use of body whorl in Gastropoda.

mm., the maximum diameter of the individual, and UT 695 appears to have been septate through at least 75 mm. As in many Mortoniceratinae the costation and tuberculation are coarser and more widely spaced on the body chamber.

Preservation of all three specimens is such that a suture could not be satisfactorily reproduced.

Measurements

UT 695; approximately ½ volution at a diameter of about 75 mm.

108			UT 10064 (holotype)					
100	32.0	37.0	43.0	0.86	38	2	2	17pr
75	30.5	40.0	50.5	0.79	40	0	2	19pr
60	35.0	38.5	50.0	0.77				
50	40.0	39.5	47.0	0.83				
40	42.5	37.5	47.5	0.79				
			UT 10824					
88	29.5	38.0	49.5	0.77	34			
75	30.0	39.5	53.0	0.75				
60	33.5	41.0	52.0	0.79				
37	36.5	42.0	55.5	0.76	28±			
20	30.0	42.5	52.5	0.81				

Observations.—*Durnovarites adkinsi*, n. sp., is the first really authentic *Durnovarites* to be described from Texas. It is so close to *D. perinflatum* (Spath) that there can be no question that these two species are congeneric; *D. adkinsi* could be considered a geographic subspecies of *D. perinflatum*. The ribs are rounder and not as sharp in the former, but the Texas specimens are internal molds which may account for the rounded costae (e.g., Spath's 1932 illustration of *D. perinflatum* [pl. 40, fig. 2] also shows rounded costae). The flanks of *D. perinflatum* are less tumid in whorl section, and converge more rapidly toward the venter than in *D. adkinsi*. The young of *D. perinflatum* are much more coarsely ornate (cf. Spath, 1932, pl. 40, fig. 52b) than are the young of *D. adkinsi*. UT 695 has a somewhat different whorl section than the holotype of *D. adkinsi* and may not belong to this species, but the lack of a larger number of good specimens prevents a final decision at this time.

Although Spath (1932) ostensibly named *Durnovarites* "for the late quadrituberculate *perinflata* group," he made a more evolute, more spinose species, *D. subquadratum*, the type species. The groups of *D. subquadratum* and *D. perinflatum* show a somewhat different ontogenetic development. Of the species Haas (1942) allied to this group, *Pervinquieria bassleri* and *P. ferecostata*, the former he associates with *Hysteroceras varicosum*, making it older than known species of *Durnovarites*. The two species described by Haas also have finer costation on the juveniles than do *D. perinflatum*, *D. adkinsi*, or *D. subquadratum*. Species of similar development to those described by Haas, from just above the *varicosum* zone equivalents in Texas, have no relation to *Durnovarites* but represent some side branch of *Pervinquieria*.

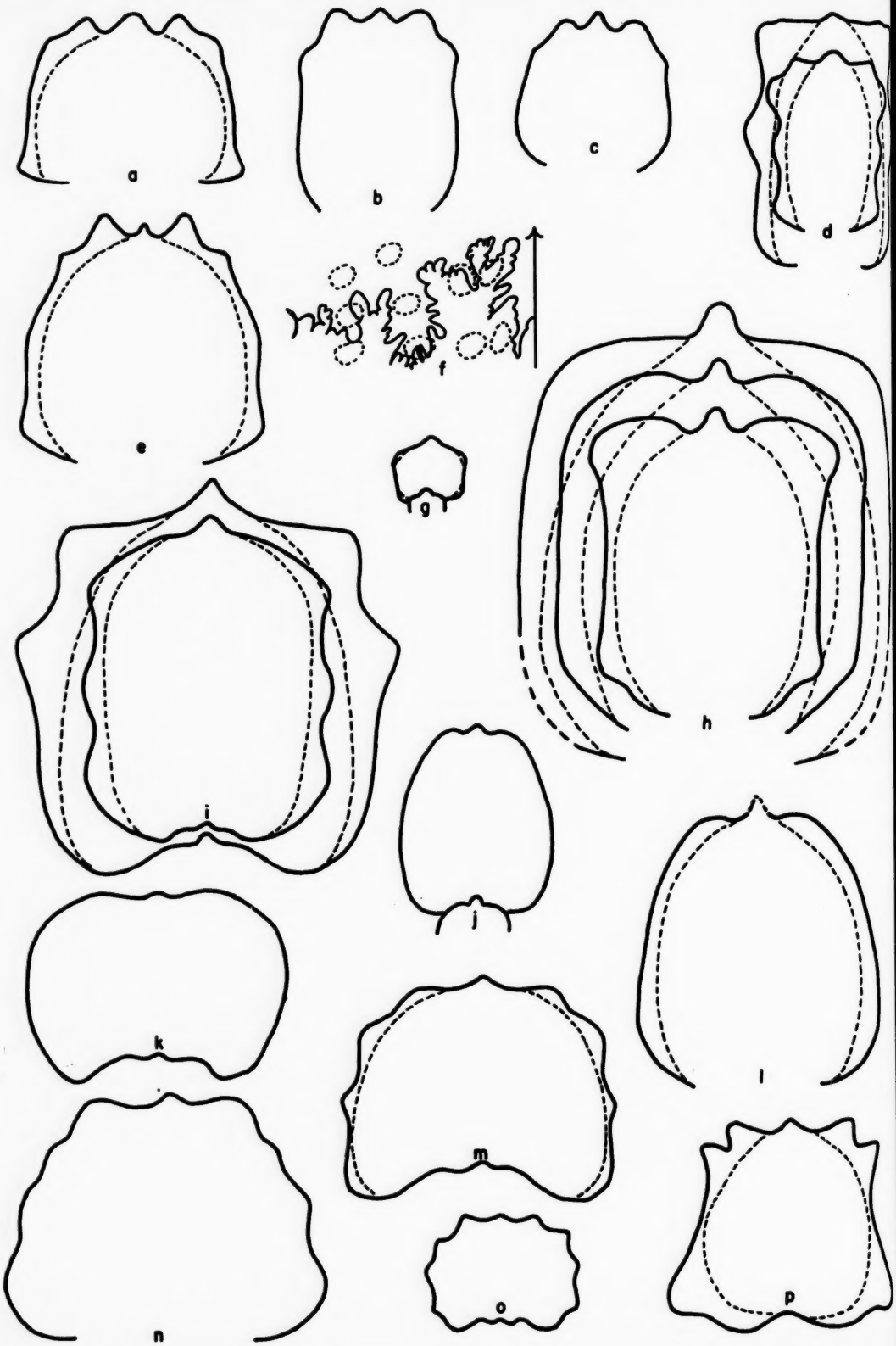
Horizon and locality.—*D. adkinsi*, n. sp., is known so far only from Travis County, central Texas, where it occurs with *Drakeoceras dellensis*, n. sp., *D. gabrielensis*, n. sp., *Turrilites brazosensis* (Römer), and an undescribed species of *Stoliczkaia*. It is known only from the lower part of the zone of *Turrilites brazosensis* and the upper part of the zone of *Drakoceras drakei*, upper part of the Georgetown limestone, Travis County.

Genus PERVINQUIERIA Böhm, 1910

(=*Inflaticeras* Stieler, 1921; =*Subschloenbachia* Spath, 1922; =*Ophryoceras* Van Hoepen, 1942; =*?Rusoceras* Van Hoepen, 1946; =*Collignonia* Van Hoepen, 1951; =*Omocrateceras* Van Hoepen, 1951; =*Styphloceras* Van Hoepen, 1951)

Type species: *Ammonites inflatus* J. Sowerby.

This genus needs little further designation of characteristics, it has been described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and emended so often. If the subgenera of Spath (1932) are removed (i.e., remove *Cantabrigites*, *Angolaites*, *Mortoniceras* [=*Leonites*], and *Durnovarites*) the genus then consists of several groups of species which seem to be fairly closely knit, providing the groups of "*Pervinquieria*" *barbouri* Haas and "*Elobiceras*" *serratescens* (Cragin) are also excluded. The two best known species groups are those of *P. inflata* (Sowerby) and *P. rostrata* (Sowerby), the former having mortonicerine costation in the very young, becoming *kiliani*-like in the early stages. In the group of *P. rostrata* mortonicerine costation may be entirely absent, *kiliani* (pervinquieriine) costation being present throughout the juvenile stages. The *P. inflata* group is weakly trinodose to strongly trinodose; the *P. rostrata* group is more strongly trituberculate in the adult.

A third group of *Pervinquieria* is allied to *P. rostrata*, differing mainly in the adult form. This group has been described by Van Hoepen under the generic name *Ophryoceras* (Van Hoepen, 1942). The group is similar to *P. rostrata* in the early costation, but in the adult the umbilical tubercles become reduced, the flank tubercles become very weak or disappear altogether, and the shoulder tubercles become extremely prominent and peculiar (e.g., *Ophryoceras jugosum* Van Hoepen, 1942). This development is entirely different from that of *Pervinquieria orientalis* (Kossmat, 1898) which belongs to the group of *P. rostrata* (Sowerby).

The forms described by Van Hoepen (1951b) under the generic names *Styphloceras* and *Omocrateceras* are pervinquieriines with hyper-nodosity, whereas the forms described under *Collignonia* Van Hoepen (1951b) constitute a fifth group in which the tuberculation is reduced, particularly the median or flank tuberculation, and in which the ribs trend forward on the venter in long, bullate, extremely weak ventral tubercles; and this group is unlike a sixth group typified by *P. fissicostatum* Spath, 1932, in which the juvenile ribbing is more *kiliani*-like than in the species grouped under *Collignonia* by Van Hoepen. *P. fissicostatum* then belongs to a sixth group which may include all of the forms included in the genus *Rusoceras* by Van Hoepen (1946a), except perhaps *R. nothum*, the type species of *Rusoceras*.

The validity of the Van Hoepen genera has been debated in arguments that do not always do credit to the authors involved. The present writer is withholding judgment but believes that there must be one large genus *Pervinquieria* or a number of smaller genera. If *Craginites*, n. gen., *Durnovarites*, *Goodhallites*, *Cantabrigites*, *Mortoniceras*, *Spathiceras*, *Deiradoceras*, *Arestoceras* Van Hoepen (1942), *Neokentroceras*, *Elobiceras*, the group of "*Pervinquieria*" *barbouri* Haas (1942), *Mimeloceras* Van Hoepen (1946a), and *Drakeoceras*, n. gen., be removed from

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TEXT-FIG. *1*

a—*Drakeoceras georgetownense*, n. gen., n. sp. Whorl section of holotype, ×1, at 75 mm. diam.; UT 863.

b—*Angolaites* sp. aff. *A. gregoryi* (Spath, 1922) [holotype of *A. vicina* (Haas, 1942)]; figure from Spath's pl. 3, fig. 2c.

c—*Angolaites* cf. *A. angolaense* (Boule, Lemoine, & Thevenin, 1907); figure after Spath (1922, pl. 4, fig. 9b).

d, *f*—*Pervinquieria whitneyi*, n. sp. Holotype, ×1; UT 10530. *d*, whorl sections (crushed) at 60 and 100 mm. diam.; *f*, suture.

e—*Drakeoceras drakei*, n. gen., n. sp. Whorl section, ×1, BEG 2451.

g, *k*, *m*—*Durnovarites adkinsi*, n. sp. Whorl sections, ×1. *g*, at 18 mm. diam.; UT 10824. *k*, at ca. 75 mm. diam.; UT 695. *m*, holotype, at 82 mm. diam.; UT 10064.

h—*Deiradoceras amsburyi*, n. sp. Whorl sections of holotype, ×1, at 150, 200, and 250 mm. diam.; UT 1341.

i—*Pervinquieria smedalae*, n. sp. Whorl sections of holotype, ×1, at 160 and 200 mm. diam.; UT 10106.

j—*Prohysteroceras wordiei* Spath, 1922. Whorl section taken from Spath's pl. 3, fig. 4b.

l—*Prohysteroceras atchisoni*, n. sp. Whorl section of holotype, ×1, at 125 mm. diam.; UT 10529.

n—*Durnovarites* sp. aff. *D. perinflata* (Spath, 1922). After Spath, p. 114, fig. 1a.

o—*Durnovarites depressa* (Spath, 1922). After Spath, 1922, p. 114, fig. 2b.

p—*Schloenbachia* sp. M. Adkins & Winton, 1920, ×1. After Adkins & Winton, pl. 5, fig. 3. It cannot represent the same species as their pl. 5, fig. 4, the whorl section of which is illustrated as Text-fig. 2–1 of this paper.

Pervinquieria Böhm, my catalogue still shows 103 trivial names preceded by *Pervinquieria*. Although some of these are probably synonyms, my records must also be incomplete. If taxonomy is the science of orderly classification and arrangement, *Pervinquieria*, even after the removal of all of the above taxa, is still too inclusive, for it presents neither classification nor arrangement in any form; in fact, without further breakdown into genera, subgenera, or species groups, it is unmanageable, being the catch-all of Albian Mortoniceratinae. This is a regrettable state for what Böhm (1910) must have intended to be a usable taxon. On the other hand our incomplete record, and therefore lack of knowledge, seems to require such polyphyletic (catch-all) taxa.

PERVINQUIERIA SMEDALAE, n. sp.
Pl. 2, fig. 2,5; Text-fig. 1i

Holotype.—UT 10106, from the *Drakeoceras lasswitzi* zone, Georgetown limestone, Berry Creek, Williamson County, Texas.

Specific characters.—Oligogyral, concentrumbilicate, sublatumbilicate, gradumbilicate, carinate. Intercostal section higher than wide, H/W roughly 1.1 to 1.15. Costal section higher than wide at a diameter of 150 mm. with H/W equal to about 1.0 on the body chamber (particularly at a diameter of 200 mm.). At a diameter of 150 mm. the costal section is arched ventrally; at a diameter of 200 mm. the venter is almost flat in costal section.

From what can be seen of costation prior to the body chamber juvenile costation is pervinquieriine, the first ¼ of the last volution containing costae quite similar to those of *Pervinquieria kiliani* (Lasswitz), but more robust; that is, the costae are closely spaced, trinodose, slightly prosiradiate, straight, mostly bifurcating from umbilical tubercles; here and there occurs a single secondary rib without an umbilical tubercle. At this stage (diameter of 150 mm.) the costae are wider than the intercostae. There is only one bifurcating pair of costae beyond the 160 mm. diameter. Since septation ceases at 150 mm., the change from densicostate to paucicostate occurs at the beginning of the body chamber. This change is very marked. Of 27 costae on the last volution, 11 are on the first ¼ volution and 16 on the last ¾ volution, or 17 are on the penultimate ½ volution and 10 on the ultimate ½ volution. On the last half of the body whorl, which is broken just orad of the rise in the keel to meet the rostrum, all ribs are single, and intercostae are at least twice as wide as the costae. Ribs are prosiradiate on the penultimate ½ volution, rectiradiate on the ultimate ½ volution, except the last two ribs which are prosiradiate.

The rostrum appears to be raised as in *Pervinquieria inflata* (Sowerby) (illustrated by Spath, 1932, p. 403, fig. 173d).

The costae are trinodose, and tubercles are nodate, the umbilical tubercles becoming bullate on the last ½ of the body whorl. The flank tubercle is ventrad of mid flank, about ⅗ of the flank from the umbilicus. The shoulder tubercles do not rise ventrad but are projected laterad, emphasizing the height of the already high keel.

The body chamber encompasses about 290 degrees of the last volution, and the preceding whorl is overlapped so as to just cover the shoulder tubercle.

Measurements of holotype

217					27	12	1 7pr
200	44.5	29.0	26.5	1.10			
150	43.0	32.5	28.5	1.14			

Observations—Pervinquieria smedalae, n. sp., resembles none of the Gault species so far described, being more like *P. stoliczkai* (Spath, 1922, p. 120, fig. 1–2) than any others in the spacing of the costation, but without the ventral prolongation of the shoulder tubercles. The tubercles are positioned somewhat as in the holotype of *Pervinquieria rostrata* (Sowerby) (Spath, 1932, p. 402, fig. 136), but the flank tubercle is less prominent and of different shape, and the umbilical tubercle much more nodate. The costation actually recalls that figured by Stoliczka (1865, pl. 29, fig. 4,4a) except the flank tubercle is displaced more ventrad and is less spinose in *P. smedalae*.

Horizon and locality.—See above under Holotype.

PERVINQUIERIA WHITNEYI,* n. sp.
Pl. 2, fig. 3,4; Pl. 3, fig. 1; Text-fig. 1d,f

Holotype.—UT 10530, from the zone of *Oxytropidoceras bravoense*, Georgetown limestone, at Round Rock, Williamson County, Texas.

* Atchison, MS, 1954, University of Texas thesis, illustrated this species in his Pl. I, fig. 2.

Specific characters.—Oligogyral, concentrumbilicate, sublatumbilicate, gradumbilicate, carinate, intercostally convexifastigate; whorl section higher than wide (crushing of the specimen exaggerates this feature, and the effects of crushing have not been removed from Text-fig. 1d), moderately costate up to a diameter of 80 mm., paucicostate in later whorls; costae rectiradiate, quadrituberculate on the last whorl and probably earlier whorls, there being a double shoulder tubercle, of which the ventral element is clavate and the dorsal element is bullate; umbilical tubercle nodate to about 85 mm., then bullate; on the last half of the last (preserved) whorl the two shoulder tubercles merge into one large tubercle which is directed laterad rather than ventrad. Costation is typically pervinquieriine except for the extra shoulder tubercle.

The holotype of *P. whitneyi*, n. sp., is septate through all of its 125 mm. diameter. The sutures are not well preserved (Text-fig. 1f), and vary from one to the next because of the peculiar tuberculation. The suture is mortoniceratine with a long ventral lobe and narrow, short, ventral saddle; the first lateral saddle is wide, the first lateral lobe is normal but with secondary elements distorted by closely spaced tubercles; second lateral lobe present, but small.

Measurements of the holotype

125	40.0	37.0	21	20	1	0
100	38.5	38.5	24	19	3	1pr
75	37.0	44.5	27			
60	38.5	42.5				
50	31.0	34.0				

Observations.—*Pervinquieria whitneyi*, n. sp., is the oldest *Pervinquieria* so far recorded from Texas. It would therefore be expected to be atypical, if it can be even properly placed in that genus. *P. whitneyi* has more the appearance of the *P. rostrata* group than the *P. inflata* group, but the double shoulder tubercle is atypical. The typical flank ribbing of *Pervinquieria* is present. In addition to the general appearance, the neanic pervinquieriine costation and the whorl sections prevents it from being included in the later quadrituberculate genus *Durnovarites* Spath, and it differs from another geologically later quadrituberculate genus, *Angolaites*, in whorl section.

P.? nanum Spath (1933) is a quadrituberculate form questionably placed in *Pervinquieria* by that author. Van Hoepen placed such quadrituberculate forms as *P. ornata* Van Hoepen (1944) in *Pervinquieria*. Both of these species appear to be juveniles and their taxonomic position remains questionable; neither of them is closely related to *P. whitneyi*, n. sp.

Horizon and locality.—*Pervinquieria whitneyi*, n. sp., is from beds of Kiamichi age, zone of *Oxytropidoceras bravoense*, the holotype occurring in place 1.9 feet above the top of the Edwards limestone, and 2 feet below *Oxytropidoceras* cf. *O. belknapi* and 3.4 feet below the base of the zone of *Eopachydiscus brazoense*, Georgetown limestone, Williamson County, Texas. The fossil was collected at the railroad bridge across Lake Creek in southwest Round Rock. When Dick E. Atchison collected the holotype in the fall of 1953, the writer revisited the locality with him; the external mold from which the holotype had been removed was still intact in the ledge.

Genus MIMELOCERAS Van Hoepen, 1946

(= *Mimoceras* Van Hoepen, 1941, non Hyatt; = *Mimeloceras* Van Hoepen, 1944, nomen nudum*)

Type species: *Mimeloceras binodosum* (Van Hoepen, 1941) Van Hoepen, 1946.

Generic characters.—Relatively evolute, oligogyral and concentrumbilicate, widely sublatumbilicate to latumbilicate; subgradumbilicate; carinate. Juvenile costation pervinquieriine, bifurcating from a usually nodate umbilicate tubercle situated on the margin of the umbilicus. Adult costation bituberculate; single primary ribs or single primary and secondary ribs, or bifurcating at a large umbilical tubercle removed from the flank.

Observations.—*Mimeloceras* Van Heopen

* Van Hoepen (1941) first used the name *Mimoceras*, not knowing that this name was preoccupied by one of Hyatt's nautiloids. Van Hoepen (1944) then thought that he had corrected this error when he first used the name *Mimeloceras*, but this name remained a nomen nudum because of improper designation as prescribed by the Rules of Zoological Nomenclature. In 1946 Van Hoepen (1946a) still did not properly designate the type species preceding the description of further species of the genus, and by a strict application of the rules, if any now apply, the name is still a nomen nudum even though Van Hoepen's intent is perfectly clear.

is to *Deiradoceras* Van Hoepen as *Pervinquieria* Böhm is to *Mortoniceras* Meek. In other words *Mimeloceras* is the form with pervinquieriine (trinodose) juvenile costation, whereas *Deiradoceras* has mortonicerine juvenile costation. *Mimeloceras* is strongly bituberculate in the adult.

Genus DEIRADOCERAS Van Hoepen, 1931

Type species: *D. prerostratum* (Spath, 1922).

Generic characters.—Relatively evolute, oligogyral and concentrumbilicate, widely sublatumbilicate to narrowly latumbilicate; subgradumbilicate; carinate. Juvenile costation is coarse and mortonicerine, bifurcating from a tubercle located ventrad of the umbilical margin; adult ribbing as in juvenile, or single and primary, or single and primary and secondary. Primary ribs in the adult are binodose; secondary ribs with shoulder tubercles only; tubercles may be nodate or bullate. never clavate. Some species have spiral ornamentation, but this is never a generic character. Because the ribs are bituberculate the costal section is usually concave on the flanks.

Observations.—*Mimeloceras* should not be carried in synonomy with *Deiradoceras*. If *Mimeloceras* must be a synonym of something, it should be synonymous with *Pervinquieria*. *Mimeloceras* bears the same relationship to *Deiradoceras* that *Pervinquieria* bears to *Mortoniceras*. *Mimeloceras* and *Pervinquieria* have the finer, pervinquieriine (*kiliani*-like) juvenile costation, whereas *Mortoniceras* and *Deiradoceras* have the coarsely bifurcating juvenile costation of *Mortoniceras leonensis* (Conrad). If there are morphological reasons for separating *Mortoniceras* and *Pervinquieria*, those same reasons separate *Deiradoceras* from *Mimeloceras*. The arguments are not so strong for separating *Deiradoceras* from *Mortoniceras* or for separating *Mimeloceras* from *Pervinquieria*.

DEIRADOCERAS AMSBURYI, n. sp.
Pl. 4, fig. 4; Pl. 5, fig. 3; Text-fig. 1h

Holotype.—UT 1341, from near the base of the Espy formation, Ocotillo Quadrangle, east of the Chinati Mountains, Trans Pecos Texas.

Specific characters.—Oligogyral, concentrumbilicate, widely sublatumbilicate to narrowly latumbilicate, gradumbilicate, carinate; intercostal whorl section higher than wide, oval; costal section subquadrate with concave flanks at a diameter of 150 mm., flanks in costal section becoming convex by a 200 mm. diameter and continuing slightly convex to more advanced stages.

Costation bituberculate, single and primary (all ribs of the same grade) on the last whorl, bituberculate and bifurcating (mortonicerine) in part on earlier whorls; moderately costate. Costae and intercostae are about equal in width. The ventral ends of the ribs swing forward as the ventral node tapers to the venter. Costae slightly rursiradiate on the last whorl, usually rectiradiate on preceding whorls. Apertural margin straight and bounded by a rib. Rostrum is spirally coiled and short. In earlier whorls and the early part of the last whorl the bullate ventral tubercles flare out to be properly designated horns; ventral tubercules later reduced in size. Ventral and umbilical tubercles bullate throughout. Keel is high, somewhat eroded on the holotype.

The overlap does not conceal the shoulder tubercle; the shell of the holotype is septate to a diameter of 180 mm., and the body chamber occupies about 210 degrees of the last volution.

EXPLANATION OF PLATE 3

FIG. *1*—*Pervinquieria whitneyi*, n. sp. Lateral view of holotype, ×1; UT 10530. (p. 10)

2—*Drakeoceras drakei*, n. gen., n. sp. Ventral view, ×1; UT 1460, lower part of the *Turrilites brazosensis* zone, Georgetown limestone, ¼ mi. above the highway 104 bridge across Smith's Branch, 1 mi. E of Georgetown, Williamson Co., Texas; collector: K. Young, 1950. (p. 26)

3—*Drakeoceras gabrielense*, n. gen., n. sp. Ventral view, ×1; BEG 186. This is the specimen figured by Adkins & Winton (1920) in their pl. 5, fig. 4. (p. 22)

4—*Drakeoceras maximum* (Lasswitz, 1904), n. gen. Lateral view of cast of holotype in the Bur. Econ. Geol., Univ. Texas, ×½. (p. 29)

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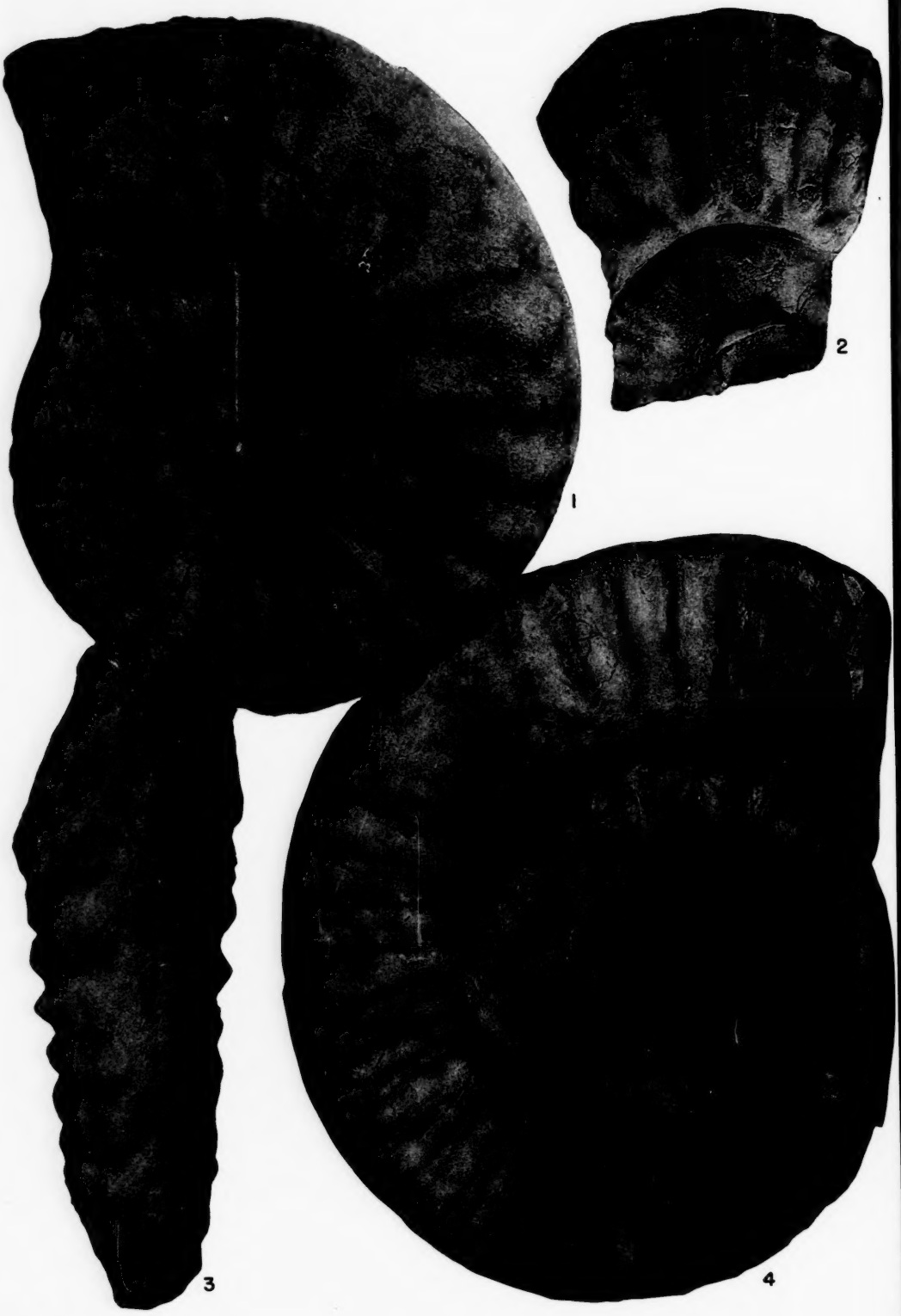
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Measurements of holotype

250	49.5	27.0	20.5	1.31	36	36	0	0
200	56.6	28.0	21.0	1.32				
150	50.0	30.0	19.5	1.55				
100	47.0							

Observations.—*Deiradoceras amsburyi*, n. sp., resembles *D. bispinosum* (Spath) so thoroughly that it might be considered a geographic subspecies, could the ages of the two species be proved comparable. The adult diameter of *D. bispinosum* (see Van Hoepen, 1941, pl. 12) is about 290 mm. Comparing other features at a diameter of 250 mm.:

	U	No. of ribs
D. bispinosum (pl. 12)	50.0	28 ±
D. amsburyi (holotype)	49.5	36 ±

Costation is alike in the two species except that it is more dense in *D. amsburyi*. The maximum diameter of *D. amsburyi* (holotype) with apertural margin intact is about 256 mm. The maximum diameter of *D. bispinosum* (Van Hoepen's pl. 12) with apertural margin intact is about 290 mm. in *D. bispinosum* the section is wider at the umbilicus than at the venter, and at a diameter of about 290 mm. H/W = 1.0 costally.

Horizon and locality.—See above, under Holotype. The biostratigraphy of the Washita rocks is as yet incomplete in this area, but *D. amsburyi* is known to occupy a level above the zone of *Craginites serratescens* (Cragin). It is suspected to occupy a level about the zone of *Pervinquieria kiliani* (Lasswitz).

Genus PROHYSTEROCERAS Spath, 1922

Type species: Prohysteroceras wordiei Spath, 1922.

Generic characters.—Evolute ammonitic cones with ribs flexiradiate or concave orad in the adult; dipolocerine juvenile costation. Adult costation may be of two or three grades, or of only one grade as in the type species. Forms with ribs intercalating at or ventrad of mid flank should probably go into the genus *Neoharpoceras* Spath, 1921. The whorl sections of species of *Prohysteroceras* are oval or elliptical.

Remarks.—Few typical members of this genus have so far been described from Texas. There are forms in the boundary area with *Goodhallites* Spath, 1932, and undescribed forms in the boundary area with *Neoharpoceras* Spath, 1921. Most of the species included in *Prohysteroceras* by Adkins (1928) are now assigned to *Goohdallites* Spath; these are *Goodhallites whitei* (Böse), *G. burckhardti* (Böse), and questionably *G. austinensis* (Römer). *"Schloenbachia" wenoensis* (Adkins, 1920) has been assigned to *Spathiceras* Whitehouse, 1926. The species assigned to *Prohysteroceras* by Haas (1942) include *P. wordiei* Spath and other species which appear closer to some of the Texas species now assigned to *Goodhallites* [e.g., Haas reports *"P." decipiens* Spath, *"P."* cf. *dubium* Spath, and *"P." hanhaense* Haas (1942)].

Described below is a species which is more closely related to the type species of *Prohysteroceras* than are most Texas species previously ascribed to this genus.

PROHYSTEROCERAS ATCHISONI n. sp.

Pl. 2, fig. 1; Text-fig. 11

Holotype.—UT 10529, from the Georgetown limestone, *Eopachydiscus brazoense* zone, on Lake Creek, Round Rock, Williamson County, Texas.

EXPLANATION OF PLATE 4

FIG. *1*—*Drakeoceras drakei*, n. gen., n. sp. Lateral view, ×1; UT 1460. (p. 26)

2—*Craginites*, n. gen., n. sp. Lateral view, ×1; UT 1340, questionably from the zone of *Craginites serratescens*, from the "Kiamichi" formation, Indio Mountains, SW ¼ NE ¼ sec. 67, Blk 3, G. C. & S. F. RR Co., Hudspeth Co. Texas; collector: Bostwick, 1952. (p. 18)

3—*Craginites serratescens* (Cragin, 1893), n. gen. Ventral view ×1; BEG 2402, from the *Craginites serratescens* zone, type locality of the Duck Creek formation, 2½ mi. N of Denison in Duck Creek (east branch), just below Frisco RR tracks, Grayson Co.; collector: W. S. Adkins, 1927. The individual is a topotype. (p. 15)

4—*Deiradoceras amsburyi*, n. sp. Lateral view of holotype, ×½; UT 1341, from near the base of the Espy formation, Ocotillo Quadrangle, Trans Pecos Texas. (p. 12)

Specific characters.—Oligogyral, concentrumbilicate, sublatumbilicate, subgradumbilicate, carinate, convexifastigate; whorl section oval, higher than wide, with convex flanks, the flanks tapering ventrad, resulting in the widest part of the shell being just ventrad of the umbilicus. The shell is moderately densicostate with about 38 ribs per volution at a diameter of 150 mm.; costae rectiradiate. Adult costae alternate primary and secondary with very low bullate umbilical tubercles on the primary ribs. No shoulder tubercles or flank tubercles are discernible. The costae were beaded with spirally arranged papillae on the last whorl, at least, but the preservation is so poor that these do not show in the illustration. The shell is evolute and the overlap barely extends past the rounded shoulder. Preservation is so poor it is difficult to determine the septate portion, but the shell may have been septate past a diameter of 150 mm.

Measurements of holotype

150	46.5	30.5	22.5	1.35	38	20	18	0
100	42.0	33.5	24.5	1.37				
75	38.5	37.5						

Observations.—*Prohysteroceras atchisoni*, n. sp., is the first species from Texas which can be referred to this genus in a restricted sense, although it may be older than the type species from Angola. Haas (1942) states only that *Prohysteroceras* is younger than *Hysteroceras*. The juvenile costation is similar to that of *Craginites*, n. gen. The whorl section compares very favorably with that of *P. wordiei*.

Horizon and locality.—See above, under Holotype.

Genus CRAGINITES n. gen.
Type species: *Craginites serratescens* (Cragin, 1893) [=*Schloenbachia leonensis* var. *serratescens* Cragin, 1893].

Generic characters.—Coiling is oligogyral, concentrumbilicate, subangustumbilicate, gradumbilicate, alticarinate; U=32–44; these ammonites appear to be marked by spiral ornamentation throughout the more adult whorls; the ribs are alternating in the adult, being primary and secondary, with bullate umbilical tubercles on the primary ribs. The bullate ventrolateral (shoulder) tubercles seem always to bear two large clavate nodes in the adult. The whorl height is equal to or greater than the whorl width both intercostally and costally. Juvenile ribbing is dipolocerine. The young whorls are flat-flanked, with height greater than width whereas the young whorls of *Dipoloceras* and its allies are tumid with rounded flanks.

Observations.— Species of this group have been included under such varied genera as *Pervinquieria* Böhm, *Elobiceras* Spath, and *Prohysteroceras* Spath. The genus is quite distinct in ribbing and whorl section from *Prohysteroceras* if *P. wordiei*, the type species, is any indication. *Craginites*, n. gen., does not have the coarse, bifurcating costation of *Mortoniceras* nor the bifurcating, trinodose ribbing so characteristic of *Pervinquieria*. If the forms without club-shaped ribs be removed from the geological-ly younger(?) and otherwise homogeneous *Elobiceras*, which is more involute, the latter group then appears to encompass a tight, distinct genus which is more involute than *Craginites* (U=25 plus or minus in such an interpretation of *Elobiceras*), and in which the ribs are club-shaped, expanding regularly in width from the umbilicus ventrad. If Spath's (1942) reading of *Elobiceras* is correct, *Craginites* is somewhat older.

Craginites has been separated from *Rusoceras* Van Hoepen (1946a) because the latter has a trinodose (pervinquieriine) stage where the former does not; *Rusoceras* lacks the double shoulder tubercle. "*Elobiceras*" *browni* Haas (1942) which Van Hoepen (1951a) says is a *Rusoceras* has also only the single shoulder tubercle, but lacks the pervinquieriine juvenile costation.

Localities and horizons.— In Texas *Craginites* occupies a zone at the base of the Georgetown formation from McLennan County north (lower Duck Creek), and occurs rather sporadically in Bell County (Adkins & Arick, 1930). It occurs in the Fort Stockton region at the same stratigraphic level and also farther west in Texas, exam-

ples coming from the southern Eagle (Indio) Mountains, Sierra del Prieta, the Shafter area, and Pinto Canyon. In the area west of Fort Stockton the genus occurs in what is mapped as "Kiamichi," except at Sierra del Prieta, where it occurs in the basal "Duck Creek sandstone" of Adkins (1933) and at Pinto Canyon where it occurs in the formation overlying the "Kiamichi" (Amsbury, 1957).

The Texas representatives appear to occupy a definite zone in the Upper Albian at about the lower *varicosum* zone level; this zone in Texas is the zone of *Craginites serratescens* (Cragin).

Measurements

BEG 19515; the holotype, is a crushed outer whorl on which measurements can not be trusted

			BEG 17433					
137	43.5	37.0	28.0	1.31	41	21	20	0
100	34.0	37.5	25.0	1.50	40	20	20	0
75	37.5							
60	32.5							
			BEG 2402					
150±		35.5	26.0	1.37				
			BEG 18726					
115	37.0	35.0	25.5	1.48	40±	20±	20±	0

CRAGINITES SERRATESCENS (Cragin, 1893)

Pl. 4, fig. 3; Pl. 5, fig. 1,2,4; Text-fig. 2a,d,e,p

Schloenbachia leonensis var. *serratescens* CRAGIN, 1893, Geol. Surv. Texas, 4th Ann. Rpt., p. 241.
Elobiceras serratescens (Cragin). ADKINS, 1927, Univ. Texas Bull. 2738, p. 41, 43, 44, 51, 55, 63; ADKINS, 1928, Univ. Texas Bull. 2838, p. 234.
?Elobiceras serratescens (Cragin); ADKINS & ARICK, 1930, Univ. Texas Bull. 3016, p. 43.
Elobiceras serratescens (Cragin). ADKINS, 1933, Univ. Texas Bull. 3232, p. 355.
?Elobiceras sp. BRAND, 1953, Univ. Texas, Bur. Econ. Geol., Rpt. Invest., no. 20, p. 11.

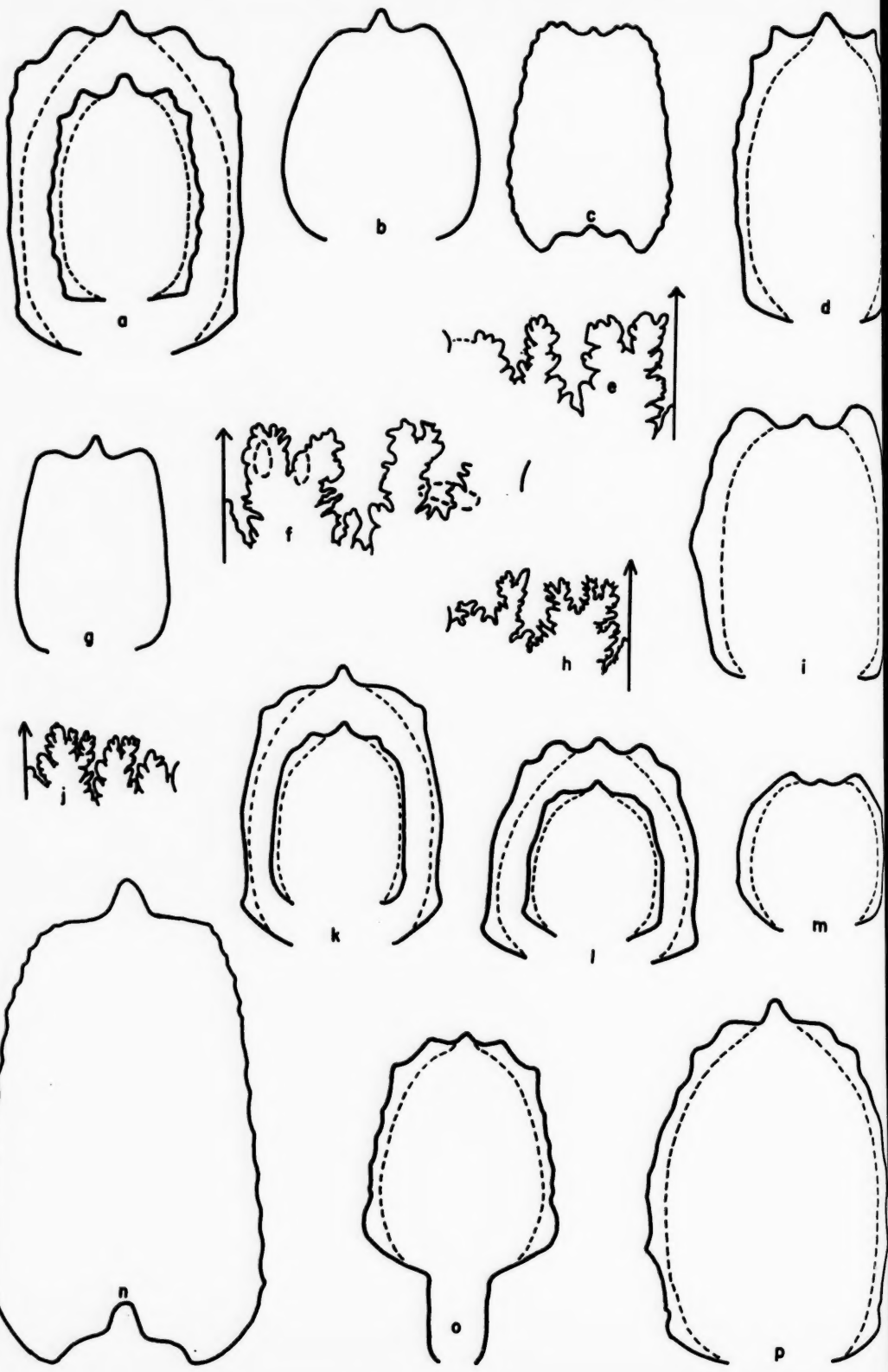
Holotype.—BEG 19515, from the lower Duck Creek formation, Duck Creek, north of Denison, Grayson County, Texas.

Specific characters.—This species has all of the characters of the genus. In addition it has flexiradiate costae in the adult; the costae alternate almost regularly primary and secondary, each primary rib bearing a bullate umbilical tubercle and a bullate shoulder tubercle which in turn has two large clavate nodes. Each secondary costa is nontuberculate at the umbilicus and bears a shoulder tubercle identical with that of each primary rib. Overlap is just dorsad of the dorsal element of the shoulder tubercle, so that neither element of this tubercle is visible except on the outer whorl. BEG 17433 is septate throughout its 137 mm. diameter, but BEG 18726 is septate only to a diameter of 85 mm. BEG 2402 is a fragment of a large individual, the fragment being non-septate. The aperture of the species is as yet unknown.

The suture is mortoniceratine, but not sufficiently preserved on any specimen for good reproduction.

Observations.—*Craginites serratescens* was named by Cragin (1893) as a variety of "*Schloenbachia*" *leonensis* (Conrad, 1857). The variety was not mentioned as new, but his writing is the first mention of "*serratescens*" in conjunction with mortoniceratine ammonites in Texas. Since that publication the species has been mentioned in the literature by Adkins (1927, 1928, 1933) as *Elobiceras serratescens* (Cragin) and, insofar as the writer can determine, correctly interpreted paleontologically and stratigraphically; but the species has never been adequately described. Cragin's only description of the species as a variety under "*Ammonites*" *leonensis*, to which it is obviously unrelated, consists of the following sentence: "In a third phase, *serratescens*, the form is strongly compressed and the outer part more lentoid than usual, the ribs low and presenting a centripetally diminishing series of seven to nine compressed tubercles." Cragin did not illustrate his "variety" and subsequent authors have not illustrated the species.

The holotype of *Craginites serratescens*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(Cragin), BEG 19515, is still extant and in the collection of the Bureau of Economic Geology. It consists of slightly less than one-half volution of a peni-adult whorl, containing fragments of sutures; thus the body chamber, at least, is absent, and how much more cannot be ascertained. There are no juvenile whorls present on the holotype. The individual has been crushed, but not as much in the central part as at the ends. The ribs are flexiradiate, but not as much as in the species of *Rhytidoceras* described by Van Hoepen (1931, 1941). The holotype can be duplicated by a large amount of material in North Texas, in the Pan Handle of Texas, and in Trans Pecos Texas.

Except for the flexuosity of the ribbing and the double shoulder tubercle *C. serratescens* (Cragin) would appear to be closely related to the group of "*Pervinquieria*" *irregulare* (Spath), which Spath (1922) leaves in *Pervinquieria* and which Haas (1942) places in *Elobiceras*, Van Hoepen (1946b) agreeing with Spath. Cragin's species is more fastigate than "*P.*" *irregulare*, and looks somewhat like some species of *Rhytidoceras* Van Hoepen (1941), except that species of Van Hoepen's genus have tumid whorls, even in the juveniles, with well rounded flanks, and lack the double shoulder turbercle. Since Haas's (1942) objections to *Rhytidoceras* and *Drepanoceras* (Van Hoepen, 1931), Van Hoepen (1951a) has pointed out that these two genera occur below the zone of *Dipoloceras cristatum*. Haas's (1942) Angola material is younger, being in part, at least, from the *dispar* zone (Spath, 1922, 1942,) ranging down to include the *varicosum* zone. *Craginites serratescens* is from the lower part of this range (probably the *varicosum* zone), occurring above any of the *Dipoloceras* spp. described from Texas (Fredericksburg group) (Scott, 1928), and occurring between the zones of *Oxytropidoceras bravoense* and *Eopachydiscus brazoense*. If Spath's (1942) interpretation of the range of *Elobiceras* is correct, *C. serratescens* is older, but might provide an ancestor.

C. serratescens (Cragin) differs from Haas's group of "*Elobiceras*" *irregulare* (Haas, 1942, non Spath, 1922) in possessing slightly flexuous ribs, whereas the ribs of *E. irregulare* Haas and related species are arcuate (concave orad) [e.g., *Pervinquieria arietiforme* (Spath) var. *elegans*, Haas, 1942, pl. 20, fig. 4a], as are the ribs of other species of *Craginites* from Texas. Other Angola species have slightly flexuous ribs [e.g., *P. arietiformis* (Spath) in Haas, 1942] or straight ribs. The venter of *Pervinquieria irregulare* (Spath) is not broad, with ventral sulcae is in that of *P. inflata* (Sowerby), and unlike the adult of the latter the costae of *P. irregulare* project orad on the venter, as do those of *Craginites serratescens* (Cragin).

Neither "*Elobiceras*" *irregulare* Haas nor "*Pervinquieria*" *irregulare* (Spath) fit easily into *Elobiceras*, *Prohysteroceras*, or *Pervinquieria*. In attempting to make such "fits" Haas (1942) ended with *Elobiceras elobiense* (Szajnocha), the type species of the genus, as atypical of *Elobiceras* and with

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TEXT-FIG. 2

a,d,ep—*Craginites serratescens* (Cragin, 1893), n. gen. *a*, whorl sections, ×1, at 100 and 150 mm. diam.; BEG 17433. *d,e*, whorl section and suture, ×1; BEG 18726, 2 feet above the Kiamichi-Duck Creek boundary, zone of *Craginites serratescens*, 1½ miles south of Blum, Hill Co., Texas, Bur. Econ. Geol. loc. 109-T-6; collector: B. J. Kummel. *p*, whorl section, ×1; BEG 2402.

b—"*Pervinquieria*" sp. aff. "*P.*" *inflatiforme* (Szajnocha). From Spath (1922, pl. 4, fig. 8b).

c—*Elobiceras lobitoense* Spath, 1922. After Spath's fig. 2c.

f,o—*Craginites*, n. gen., n. sp. Suture and whorl section (slightly crushed), ×1; UT 1340.

g—"*Pervinquieria*" *striatum* (Spath, 1922). From Spath's pl. 3, fig. 3b.

h,l—*Drakeoceras gabrielense*, n. gen., n. sp. Suture and whorl sections, at 50 and 87 mm. diam., ×1; BEG 186.

i—*Elobiceras lenzi* (Szajnocha). From Szajnocha, 1885.

j—*Drakeoceras dellense*, n. gen., n. sp. Suture, ×1; unnumbered specimen from the top of the zone of *Drakeoceras drakei* at Pease Park, Georgetown formation, Shoal Creek, Austin, Texas.

k—*Drakeoceras lasswitzi*, n. gen., n. sp. Whorl sections of holotype, ×1, at 60 and 100 mm. diam.; BEG 18679.

m—*Angolaites gracilis* (Haas, 1942). After Haas's pl. 13, fig. 4c.

n—"*Elobiceras*" *arietiforme* Spath, 1922. From Spath's pl. 2, fig. 6b.

Prohysteroceras wordiei Spath, the type species of that genus, atypical of *Prohysteroceras*. The species of the group of "*Pervinquieria*" *irregulare* Spath are similar to the fossils herein described under *Craginites*, n. gen., except that the Texas species all have the pronounced double shoulder tubercles, a character not present in the Angola species. Neither does Van Hoepen's South African material contain any "*Elobiceras*-like" ammonites with double shoulder tubercles. Whether these African species will eventually be determined to fit into the *Craginites* lineage, into something like *Rusoceras* Van Hoepen (1946a), or require a new genus, must be determined by a revision of that material.

Horizon and localities.—Craginites serratescens (Cragin) occurs between the zones of *Oxytropidoceras bravoense* (Böse) and *Eopachydiscus brazoense* (Shumard). It occurs in the lower Duck Creek formation from Bell County north in Texas, in the "Kiamichi" of the Pan Handle of Texas, and in the "Kaimichi" of Trans Pecos Texas; only one poorly preserved individual referable to this species has been found south of Bell County in central Texas. *C. serratescens* is associated with *Idiohamites fremonti* (Marcou), species of ammonites of the group of "*Pervinquieria*" *barbouri* Haas (1942), and some small, undescribed, keeled ammonites.

Craginites n. sp.

Pl. 4, fig. 2; Pl. 6, fig. 5; Text-fig. 2f,o

Fragments of ammonites of a species congeneric with *Craginites serratescens* (Cragin) were collected by Adams (1953) and Allday (1953) in the summer of 1952 in the Indio Mountains, Trans Pecos Texas.

This species is more flattened across the venter and H/W is not as great as in *C. serratescens*. The ribs are not as flexuous as in *C. serratescens*, and the secondary ribs do not extend as close to the umbilicus. The costal sections of the two species are quite different, that of *Craginites* n. sp., being widest at the shoulder.

Observations.—The whorl section of *Craginites* n. sp., is strikingly similar to that of *Angolaites vicina* (Haas, 1942) (see Spath, 1922, pl. III, fig. 2c, non Haas, 1942; Haas's form has only the single shoulder tubercle whereas Spath's either has a high lateral tubercle or a double shoulder tubercle; it appears to be the latter. Haas made Spath's individual the holotype of the species. Haas's illustration cannot represent a crushed form. Text-fig. 1e this paper shows how the double shoulder tubercle appears when crushed); the geologic ages and derivations of *Angolaites vicina* (Haas) and *Craginites* n. sp., are quite unrelated. Certainly the Texas species must remain in a separate genus until a reevaluation of the Angola material is completed.

Horizon and locality.—Craginites n. sp., questionably occurs in the zone of *Craginites serratescens* (Cragin). It was collected from fault blocks in the Indio Mountains (Southern Eagle Mountains) in Trans Pecos Texas. Fragments of 40 or 50 individuals are in the collection, but no individuals are complete.

Genus Goodhallites Spath, 1932

(=*Cainoceras* Van Hoepen, 1942; =*Letheceras* Van Hoepen, 1942; =*Lethargoceras* Van Hoepen, 1942; =*Aidoceras* Van Hoepen, 1946.)

Type species: *Goodhallites goodhalli* (Sowerby).

Generic characters.—Goodhallites Spath can best be described as a keeled form with

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Explanation of Plate 5

Fig. *1,2—Craginites serratescens* (Cragin, 1893), n. gen. Ventral and lateral views of holotype, ×1; BEG 19515, zone of *Craginites serratescens*, lower Duck Creek formation, 2½ mi. N of Denison in Duck Creek (east branch), Grayson Co., Texas; collectors: Taff and Leverett, 1892. (p. 15)

3—Deiradoceras amsburyi, n. sp. Ventral view of holotype, ×½; UT 1341. (p. 12)

4—Craginites serratescens (Cragin, 1893), n. gen. Lateral view, ×1; BEG 17433, 2 feet above the Kiamichi Duck Creek contact, zone of *Craginites serratescens*, 1¼ mi. S of Blum, Hill Co., Texas, Bur. Econ. Geol. loc. 109-T-6; collector: B. J. Kummel. (p. 15)

5—Drakeoceras lasswitzi, n. gen., n. sp. Lateral view, ×1; BEG 2391, zone of *Drakeoceras lasswitzi*, Georgetown limestone, 1 mi. N of Georgetown, Williamson Co., Texas. (p. 28)

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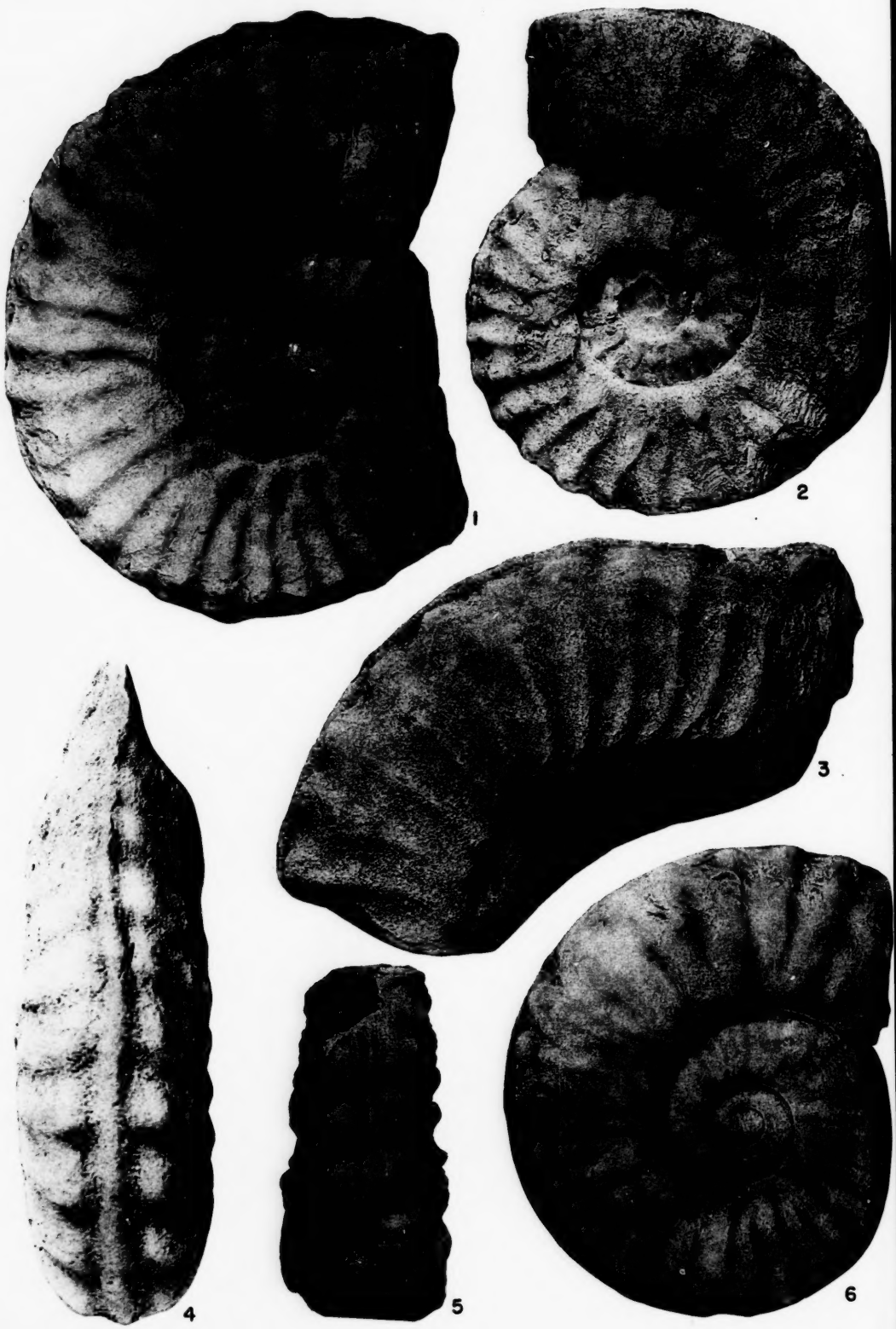
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fine costation in both adult and juvenile, tuberculation reduced, but with umbilical tubercles present, nodate or bullate. In some forms the juvenile costation may tend toward a mortonicerine aspect, but usually remains flexiradiate. U=21–36; H/W =greater than 1.0.

Observations.—The genus *Goodhallites* was first described by Spath (1932), but he included it as a subgenus of *Prohysteroceras* Spath (1922). The latter genus has been little understood and relatively few species assigned to it, perhaps as Haas (1942) suggests, this is because it is an end member of a lineage. Considering only Texas material one would think *Goodhallites* to constitute a distinct group, descended from some form with juvenile dipolocerine costation, and separate from *P. wordiei* Spath, the type species of *Prohysteroceras*. However, Angola species of *Goodhallites* such as *G. decipiens* (Spath) and *G. hanhaense* (Haas) appear closer to *P. wordiei*. Even though the transition were complete I would prefer not to use *Goodhallites* as a subgeneric unit because in number of species and individuals it is a much larger taxon than is *Prohysteroceras* s. s.

In addition to the group of *Goodhallites goodhalli* (Sowerby), there are four other groups of this genus: (1) the group of "*Schloenbachia*" *gracillima* Kossmat (1898) in which the costae are coarser, only slightly sigmoid, and in which the whorl-section is peculiarly trapezoidal. Van Hoepen (1942) described forms belonging to this group under his genus *Cainoceras*. (2) Another group, with much finer ribbing than the type species of *Goodhallites*, is typified by "*Schloenbachia*" *whitei* Böse (1910). (3) A group with straight ribs in the adult is typified by *Aidoceras jubatum* Van Hoepen (1946a), but not all of the forms described by Van Hoepen under *Aidoceras* have these straight ribs. (4) A group described under *Letheceras* Van Hoepen (1942) contains typical goodhallitids except that the costation tends to be effaced in the adults. This group includes "*Ammonites*" *propinquus* Stoliczka (1865) for which species Spath (1934) suggested generic separation might be warranted.

Texas species of *Goodhallites* include *G. burckhardti* (Böse), *G. whitei* (Böse), *G. aguilerae* (Böse), and questionably *G. austinensis* (Römer).

Genus DRAKEOCERAS, n. gen.

Type species: *Drakeoceras drakei*, n. sp.

Generic characters.—Oligogyral, concentrumbilicate, sublatumbilicate, gradumbilicate, carinate, intercostal section arched; subquadrate in adult whorl section, H/W ratio decreasing with age. Moderately densicostate in young forms, becoming almost paucicostate in adult. Juvenile costation is usually prosiradiate and always goodhallitine up to a diameter of from 60 to 90 mm. or more, depending on the species. Beyond that diameter the costation changes, rather rapidly (usually within ⅓ volution) to a bituberculate costation with mortonicerine bifurcation or with single bituberculate ribs, or with alternation of these two with each other and/or with secondary ribs tuberculate only at the ventral end. In most species the shoulder tubercle is double, even in juvenile individuals, whereas it is usually

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EXPLANATION OF PLATE 6

FIG. *1–4—Drakeoceras drakei*, n. sp., n. gen., *1*, Lateral view, ×1; BEG 2451, Weno formation, Lampasas River, at N end of Horseshoe Bend, 3 mi. SE of Belton and 1 mi. E of the Dallas highway, Bell Co., Texas. *2*, lateral view, ×1; UT 14446A, upper part of *Drakeoceras drakei* zone, Georgetown limestone, Smith's Branch, 1 mi. E of Georgetown, Williamson Co., Texas; collector: Billy Walls, 1950. *3,4*, lateral and ventral views of apertural half of body chamber, ×1; the periphery has been abnormally compressed by sedimentary processes; UT 14446, horizon, locality, collector as for UT 14446A. (p. 26)

5—Craginites, n. gen., n. sp., ventral view, ×1; UT 1340. (p. 18)

6—Drakeoceras arringtoni n. gen., n. sp. Lateral view of holotype, ×½; UT 10523, from the *Drakeoceras lasswitzi* zone, Georgetown limestone, abandoned road material pit on the Dedear Ranch, 0.3 mi. E of U. S. highway 81 and 3.0 mi. N of the Brushy Creek bridge at Round Rock, Williamson Co., Texas; collector: D. E. Atchison, 1954. (p. 30)

absent in *Goodhallites*, or when present, long, drawn out, and reduced as in *G. candollianum* (Pictet).

Observations.— I can find no species of this development previously described from other parts of the world. Van Hoepen's *Mimeloceras* species all go through a trituberculate (pervinquieriine) stage of costation and the costation and tuberculation is much more robust; juvenile *Deiradoceras* possess mortonicerine costation and the ornamentation on this genus is also much more robust than on *Drakeoceras*, n. gen. None of the groups of species discussed under the genus *Goodhallites* possesses the adult development herin described. The subquadrate whorl section in the adult with H/W ratio about equal to unity separate this group from "*Cainoceras*" Van Hoepen with trapezoidal section and flexiradiate ribs which definitely bifurcate, and the goodhallitine juvenile costation and subquadrate adult whorl section separate it from forms Van Hoepen (1951b) described under "*Pagoceras*," which has mortonicerine juvenile costation, usually a higher whorl section, and a fastigate venter. *Drakeoceras* is the only one of all of these groups with the double shoulder tubercle. Furthermore, in the species groups of *Goodhallites*, the H/W ratio increases with age (or more rarely remains about constant), whereas in *Drakeoceras* the H/W ratio usually decreases with age, quite a different ontogenetic development.

Angolaites gregoryi (Spath, 1922), with double shoulder tubercles, in the adult has single, evenly spaced costae, all extending to the umbilicus, whereas in *Drakeoceras*, n. gen., only the last few ribs on the body chamber are of this type. In addition *Angolaites* possesses a good flank tubercle, never present in *Drakeoceras*. "*A.*" *montroynaudensis* (Haas) [=*Schloenbachia* (*Mortoniceras*) *inflata* Boule, Lemoine & Thevenin, 1907, forme typique] compares with the Texas trinodosa with notched shoulder tubercle and mortonicerine juvenile costation. The variety *gracilis* Haas (1942) gave to this species does not belong in it. Both of these possess the flank tubercle and are more evolute than species of *Drakeoceras*.

Drakeoceras, n. gen., appears to have no relation to species of *Durnovarites* Spath (1932), but species of *Drakeoceras* do have the peculiar double shoulder tubercle of many species assigned to *Durnovarites* by Spath. The species of *Drakeoceras*, excepting perhaps *D. georgetownensis*, in which the inner whorls have not been observed, all start with goodhallitine juvenile costation, whereas *Durnovarites subquadratum* Spath, *D. quadratum* Spath, *D. postinflatum* Spath, *D. adkinsi*, n. sp., and probably *D. perinflatum* (Spath) all have juvenile mortonicerine costation followed by a neanic and ephebic flank tubercle.

The young of *Drakeoceras*, n. gen., have typical goodhallitine costation and the species differ largely in how early or late in the ontogeny the goodhallitine costation is replaced by adult costation. Even at the earliest diameters (e.g., 20 mm.) of *D. gabrielense*, n. sp., the notched shoulder tubercle is forshadowed by two papillae. Some juvenile forms even develop a neoharpoceran aspect with new costae intercalating at mid flank (UT 10103, Pl. 10, fig. 4). Juveniles of this genus can be separated from the juveniles of *Goodhallites* most easily on the possession of the two shoulder papillae. Nothing in Spath's *Goodhallites* or Van Hoepen's *Aidoceras*, *Letheceras*, or *Cainoceras* resembles the adults of *Drakeoceras*, nor do any of these genera show a notched shoulder tubercle at any stage. Species attributed to *Leonites* by Spath (1932), including "*Amm.*" *maximus* Lasswitz, have a notched shoulder tubercle as do some species of *Poikiloceras* Van Hoepen and *Pagoceras* Van Hoepen (1951b), some of the latter two genera having the notched tubercle becoming single in the adult (e.g., *P. adjacens* Van Hoepen, 1951b). However, all species of the above mentioned groups [except *Drakeoceras maximum* (Lasswitz)] have coarse mortonicerine costation in the young forms. Van Hoepen (1944) also attributes such forms with notched shoulder tubercles as "*Pervinquieria*" *ornata* and "*Pervinquieria*" *referta* to the genus *Pervinquieria* (Böhm). Other species described more properly under the genus *Pervinquieria* also have notched shoulder tubercles [e.g., *P. amplicostata* Van Hoepen, *P. cognata*, etc. Van Hoepen (1951b)], but the

rest of the ontogenies of these species is quite different from the Texas species of *Drakeoceras*. Notice particularly *Pervinquieria geniculatum* Van Hoepen, 1942, and *P. scobina* Van Hoepen, 1942.

Except for quadrituberculate forms belonging to *Angolaites* and *Durnovarites* the Mortoniceratinae with notched or double shoulder tubercles seem to be almost exclusively South African and North American (Texas, New Mexico, Mexico). The only exception known to the writer is *Pervinquieria ? nanum* Spath, 1933, which is a juvenile and probably belongs to some group of *Mortoniceras* s.s.

The South African and North American species with double shoulder tubercles, mentioned above, belong to the following groups: (1) The South African species, some mentioned above, with mid flank tubercles appearing very early in the ontogeny and with pervinquieriine juvenile costation; (2) there are the Texas species with juvenile mortonicerine costation and with mid flank tubercles appearing extremely late in the ontogeny, usually on the last volution as in "*Pervinquieria*" n. sp. Adkins (1928, pl. 10, fig. 2); (3) there are Texas species without flank tubercles, or virtually without them, and with juvenile mortonicerine costation as in *Mortoniceras wintoni* (Adkins, 1920); (4) the group with goodhallitine juvenile costation as in *Drakeoceras maximum* (Lasswitz); and (5) a more distant group, described above under the genus *Craginites*, which seems to be the double shoulder tubercle counterpart of "*Elobiceras*" *arietiformis* Spath (1922). As indicated earlier, however, by the approval of Van Hoepen's assignment of certain species with double shoulder tubercles to *Pervinquieria*, the presence of the double shoulder tubercle alone, or of any other tubercle for that matter, does not indicate any certain generic affinity unless it is a part of a discrete ontogeny that makes a complete picture.

Horizons and localities.—Various species of *Drakeoceras*, n. gen., occur in Texas, Upper Albian, ranging in age from the zone of *Pervinquieria kiliani*, upper Duck Creek formation, to the lower part of the zone of *Turrilites brazosenis*, Main Street formation. Species have been collected from north, central and Trans Pecos Texas.

DRAKEOCERAS KUMMELI, n. sp.
Pl. 8, fig. 2,4; Pl. 9, fig. 5

Prohysteroceras sp. aff. *austinensis* (Roemer); ADKINS, 1928, Univ. Texas Bull. 2838, pl. 11, fig. 2.

Holotype.—BEG 18727, collected by B. J. Kummel above the *Epoachydiscus brazoensis* zone, probably from the zone of Pervinquieria Kiliani, on the Brazos River near Steiner Bend, bed d, Bur. Econ. Geol., locality 109–T–11, Hill County, Texas.

Specific characters.—Oligogyral, concentrumbilicate, gradumbilicate, sublatumbilicate, carinate, flanks almost flat, costation goodhallitine, but with double shoulder tubercles. Costation becomes coarser at about 80 mm. diameter; appears to bifurcate to about 100 mm. diameter, although bifurcation is uneven; ribs, single, primary and secondary beyond a 100 mm. diameter. Adult costae slightly convex adorad.

The shoulder tubercle is low and double, bearing two large papillae, the ventral of which is faintly clavate and the dorsal of which is clavate up to about 80 mm. diameter and thereafter is nodate or slightly inclined. The holotype is septate to at least the 100 mm. diameter. Costae and intercostae are about the same width. The umbilical tubercle is bullate and pronounced; costae are prosiradiate, but not markedly. The keel is high, extending ventrad beyond the shoulder tubercles. The overlap of each whorl just conceals the dorsal element of the ventral shoulder tubercle of the preceding whorl. The H/W ratio is about 1.4, the whorl section being high throughout.

Measurements of holotype

113 (maximum)		33	2	3	14pr
100	31.5				

Observations.—*Drakeoceras*, n. gen., is apparently derived from some form of *Goodhallites* Spath, and *D. kummeli*, n. sp., occurs with species of *Goodhallites*. Were it not for the continuity of the group herein described under the genus *Drakeoceras*, with *D. kummeli* the beginning member, *D. kummeli* could as well be placed in the genus *Goodhallites* Spath. However, *D. kummeli* does have the double shoulder

tubercle which can not be observed in the illustrations of species of *Goodhallites* described by Spath. An example of *Goodhallites goodhalli* var. *tuberculata* Spath, kindly furnished me by R. Casey, has no evidence of double shoulder tuberculation, but its further resemblance to *D. kummeli* is remarkable. Since *D. kummeli* is the first of a continuous Upper Albian sequence which in Texas at least forms a coherent group, I have placed it in this new genus.

D. kummeli differs from other species of *Drakeoceras* in being more goodhallitid throughout, successively younger species, with few exceptions, successively losing their goodhallitid resemblance at earlier ontogenetic stages. *D. kummeli* more closely resembles *D. lasswitzi*, n. sp., than other Texas forms, but differs from the latter in its more flexiradiate costation, with the ribs less pronounced, especially at mid flank; *D. kummeli* also has a higher whorl section.

Horizon and localities.—See above, under Holotype. Adkins (1928, pl. 11, fig. 2) has recorded the species from the Duck Creek equivalents at University Mesa, Pecos County, Texas.

DRAKEOCERAS GABRIELENSE, n. sp.
Pl. 3, fig. 3; Pl. 7, fig. 2,3,5,6; Pl. 10, fig. 3,7; Text-fig. 2h, 3b,c,e,n

?Schloenbachia austinensis (Römer) var. *minima* LASSWITZ, 1904, p. 25 (pro parte), not pl. VI, fig. 1.

Schloenbachia sp. M. ADKINS & WINTON, 1920, pl. 5, fig. 1,4.

Holotype.—UT–10121, from the Georgetown limestone, lower part of the zone of *Turrilites brazosensis*, 1 mile north of the junction of U. S. highway 81 and Texas highway 195, on a branch of Dry Berry Creek; Williamson County, Texas; collected by R. T. Arrington, 1953.

Specific characters.—Oligogyral, concentrumbilicate, gradumbilicate, carinate; intercostal section arched; costation as in genus, changing from goodhallitine to coarser costation at about a diameter of 60 mm. At the same diameter the typical goodhallitine whorl section becomes subquadrate and H/W approaches unity. Adult costation is single, primary and secondary, with costae slightly concave aborad. The shoulder tubercle is bullate and bears two large clavate nodes (notched shoulder tubercle of Winton, 1925); the umbilical tubercle is nodate. BEG 34–2 is septate to 90 mm. and UT 10122 is septate to 108 mm. Other specimens do not have any of the living chamber preserved and all are septate, UT 10121 being septate through all of a 116 mm. diameter. Each whorl overlaps the shoulder tubercles and a few millimeters of the flank dorsad to the shoulder tubercle.

The suture is typically mortoniceratine with the secondary elements reduced. The first and second lateral saddles are well developed.

(*See Measurements on page 23*)

Observations.—*Drakeoceras gabrielense*, n. sp., differs from other known species of the genus in its aborad concavity of the adult costae and in the greater clavateness of the two elements of the double shoulder tubercle. The sharp flexiradiate costation of the adult is also distinctive. Lasswitz (1904) reported "*Schloenbachia*" *minima* from Pease Park in Austin where about 17 feet of uppermost Georgetown limestone is exposed below the Del Rio clay. He also described *Goodhallites minima* from the Missouri Pacific (I. G. N.) railroad cut at West Sixth Street in Austin. The figured specimen (1904, pl. VI, fig. 1) must be from the railroad cut because it

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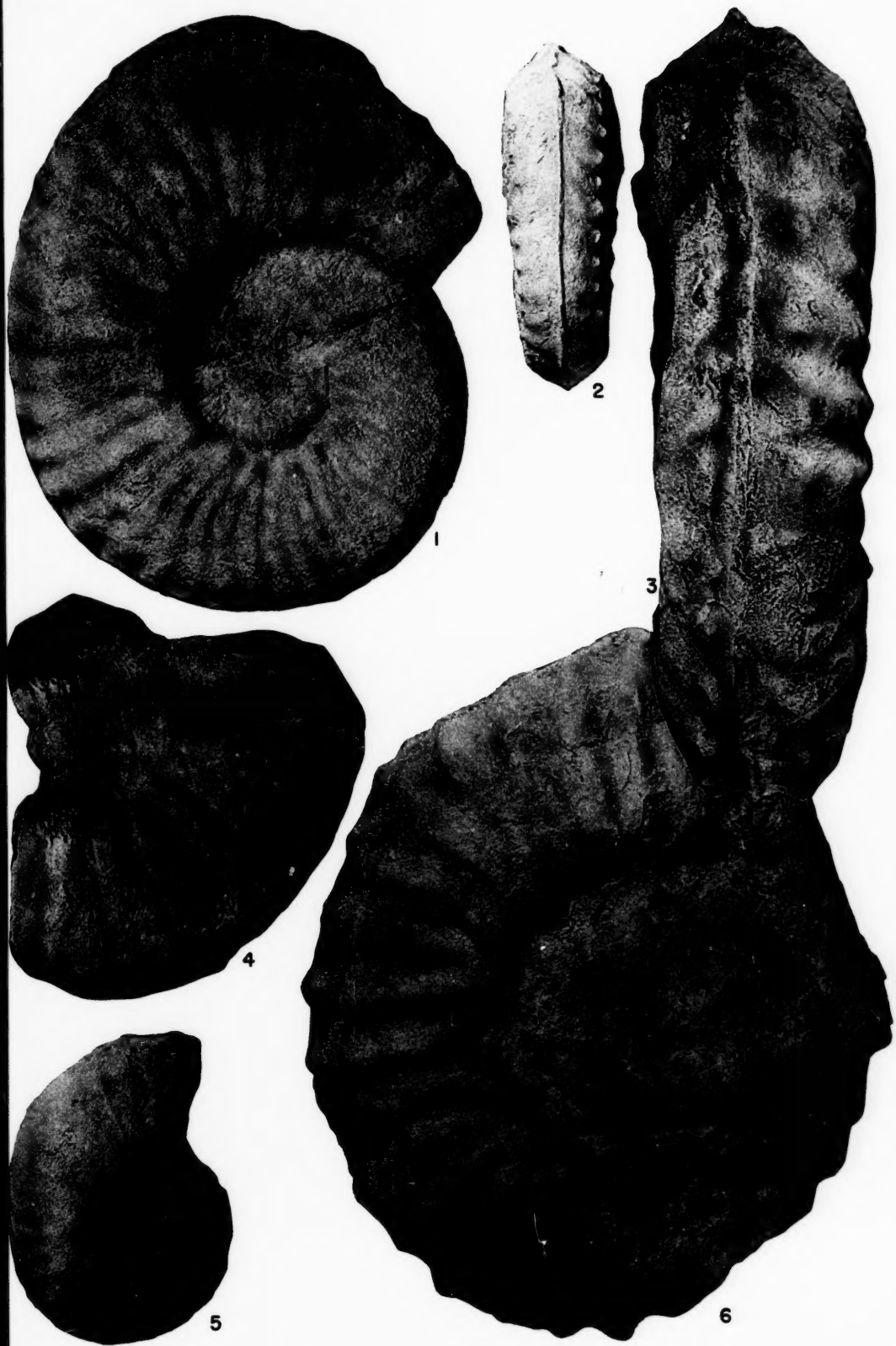
EXPLANATION OF PLATE 7

FIG. *1*—*Drakeoceras dellense*, n. gen., n. sp. Lateral view of holotype, ×1; BEG 2445A, Main Street formation, ½ mi. S of Prairie Dell, Bell Co., Texas; collector: W. S. Adkins. (p. 25)

2,3,5,6—*Drakeoceras gabrielense*, n. gen., n. sp. *2*, ventral view of juvenile specimen, ×1; BEG 3043A, from Bell Co., horizon not designated. *3,6*—lateral and ventral views of holotype, ×1; UT 10121, lower part of *Turrilites brazosensis* zone, Georgetown limestone, 1 mi. N of the junction of U. S. highway 81 and Texas highway 195, on a branch of Dry Berry Creek, Williamson Co. Texas; collector: R. T. Arrington, 1953. *5*, lateral view of juvenile specimen ×1; UT 10127; locality, horizon and collector as for UT 10121. (p. 22)

4—*Durnovarites adkinsi*, n. sp. Lateral view, ×1; UT 10824. (p. 6)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Measurements

				BEG 3043A				
60	30.0	39.0	31.5	1.27	30	0	4	13pr
50	28.0	40.0	36.0	1.11	27	0	3	12pr
40	27.5	42.5	37.5	1.30	26	0	4	11pr
30	25.0	41.5			22?	0	0	11pr
25	24.0							
20	25.0							
				BEG 186				
90	35.0	32.0	30.0	1.06	29?	9?	10?	5?pr
75	27.5	29.0	28.5	1.02				
60		22.5						
				BEG 34-2				
108					36			
				UT 10127				
55								
50	30.0	42.0	37.0	1.14	29	0	1	14pr
40	29.0	40.0	34.0	1.19				
30	26.5	38.0	30.0	1.22				
20	35.0	45.0	35.0	1.20				
				UT 10122				
117					31	13	11	4pr
100	36.5	33.5	27.0	1.24				
75	34.5	39.0						
60	35.0	45.0	33.5	1.35				

appears to be a true, but densicostate, *Goodhallites*, without shoulder tubercles, whereas the Pease Park locality exposes rocks of only the *Turrilites brazosensis* and *Drakeoceras drakei* zones, and is too high in the section for the occurrence of *Goodhallites*. The specimen reported from this Shoal Creek (Pease Park) locality was, thus, not figured by Lasswitz (1904) and is probably a *Drakeoceras gabrielense* as the writer has found examples of this species at this locality and horizon.

"*Schloenbachia*" *wintoni* Winton (1925, non Adkins, 1920) appears to be very closely related to *D. gabrielense* and might be conspecific with it. I've not seen the specimen, only the illustration (Winton, 1925, pl. 5, fig. 4). Winton's individual may be older than most individuals of *D. gabrielense*, and is slightly more densicostate at equivalent diameters.

Schloenbachia sp. M (Adkins & Winton, 1920) has been assigned to this species although it appears to be transitional to *Drakeoceras drakei.*, n. sp. Although the whorl section of the juvenile is similar to that of *Drakeoceras drakei*, the adult section and the flexiradiate adult costation is similar to that of *D. gabrielense.*

Horizon and localities.—Drakeoceras gabrielense, n. sp., is one of the two youngest species so far assigned to the genus, and with *Drakeoceras dellense*, n. sp., and *Durnovarites adkinsi*, n. sp., is one of the three youngest Mortoniceratinae in the Texas Cretaceous. *D. gabrielense* occurs in the lower

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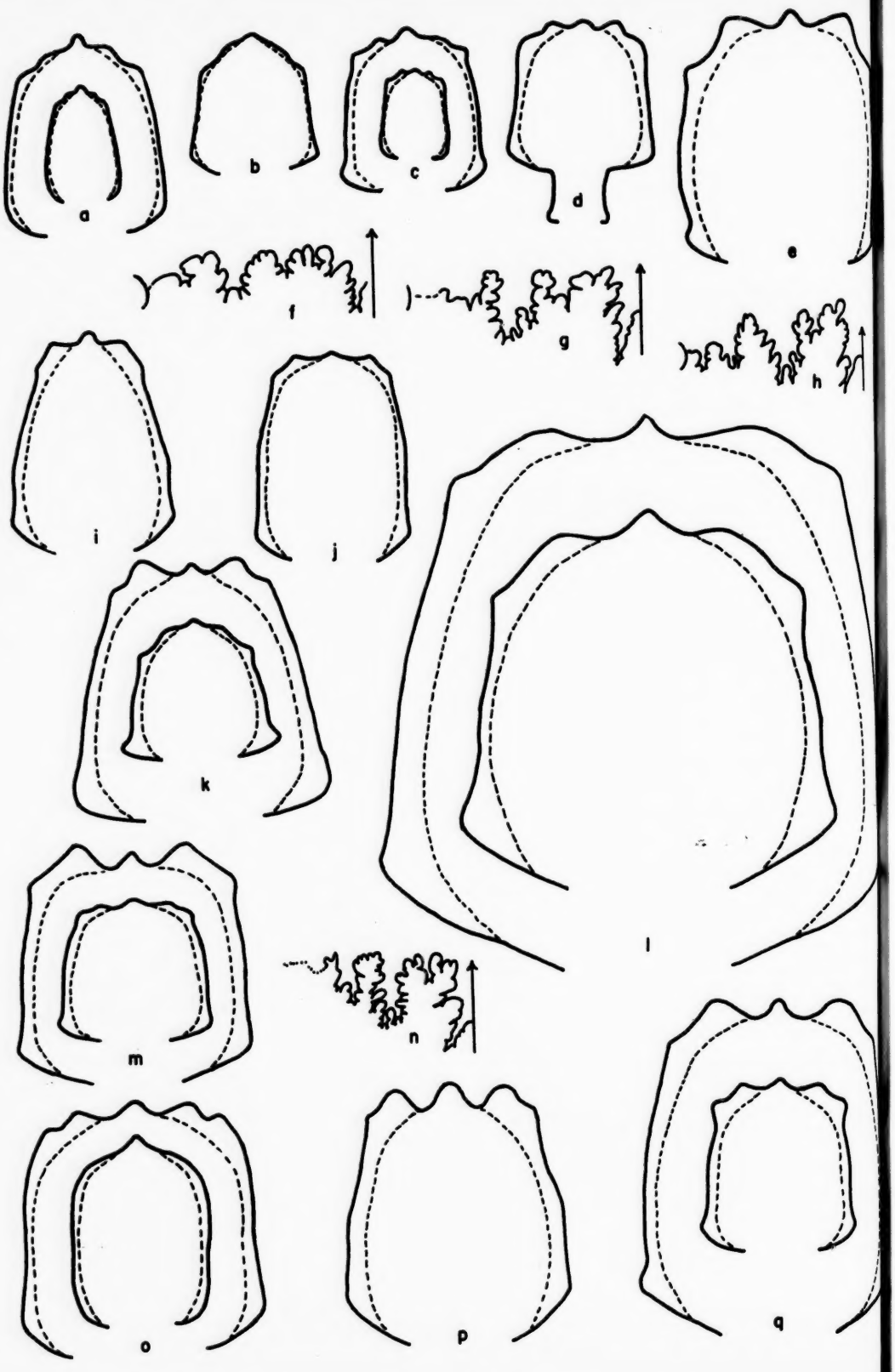
EXPLANATION OF PLATE 8

FIG. *1—Drakeoceras georgetownense*, n. gen., n. sp. Ventral view of holotype, ×1; UT 863, Georgetown formation, Smith's Branch, 1 mi. E of Georgetown, Williamson Co., Texas. (p. 27)

2,4—Drakeoceras kummeli, n. gen., n. sp. Ventral and lateral views of holotype, ×1; BEG 18727, probably from the zone of *Pervinquieria kiliani*, Duck Creek formation, bed d, Bur. Econ. Geol. loc. 109–T–11, Brazos River, near Steiner Bend, Hill Co., Texas; collector: B. J. Kummel. (p. 21)

3—Drakeoceras lasswitzi, n. gen., n. sp. Lateral view of holotype, ×1; BEG 18679, zone of *Drakeoceras lasswitzi*, top of Fort Worth formation, bed 109, Bur. Econ. Geol. loc. 109-T-6, Rock Creek, E of Blum, Hill Co., Texas; collector: B. J. Kummel. (p. 28)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part of the zone of *Turrilites brazosensis* in central Texas, along with the two species mentioned above, *Turrilites brazosensis* Römer, and a new species of *Stoliczkaia*, occurring in the upper part of the Georgetown limestone. It also occurs in the underlying *Drakeoceras drakei* zone. The species has been collected from Travis County to North Texas.

DRAKEOCERAS DELLENSE, n. sp.
Pl. 7, fig. 1; Pl. 10, fig. 4,5,9,10;
Text-fig. 2j,3a,h-j

Holotype.—BEG 2445A, from the Main Street formation, ½ mile south of Prairie Dell, Bell County, collected by W. S. Adkins.

Specific characters.—Oligogyral, concentrumbilicate, sublatumbilicate, gradumbilicate, carinate; flanks slightly arched. Costation is densicostate, moderately goodhalli-

tine to diameters of 100 mm. or more. Costae convex adorad, prosiradiate with some intercalated ribs as ventrad as mid flank. There are from 40 to 45 ribs per volution at a diameter of 75 mm., of which almost half form bifurcating pairs. The H/W ratio is from 1.3 to 1.5. The whorl section remains high throughout, having some resemblance to whorl sections of *Neoharpoceras*. A typical shoulder tubercle is non-existent, but there are two rows of papillae on the shoulder as in the juveniles of *D. gabrielense*. The dorsal of these two papillae is nodate, the ventral inclined with the forward inclination of the rib onto the venter. All individuals examined were septate, and adult forms may be larger than those of *D. gabrielense*, n. sp. Each whorl overlaps past the two shoulder papillae on the preceding whorl and onto a few mm. of the flank. Sutures are as in *D. gabrielense*.

				Measurements				
				BEG 3043B				
82 (maximum)								
75	31.5	41.5	30.0	1.38	38			
50	32.0	46.0	34.0	1.38				
				UT 10103				
75	28.5	38.5	30.0	1.29	46	1	1	22pr
60	29.5	41.5	31.5	1.31				
50	29.0	41.0	32.0	1.28				
40	27.5	41.5	27.5	1.50				
				UT 14413				
111 (maximum)					34	3	11	10pr
100	30.5	37.5	26.5	1.41	35			
75	29.5	40.0	28.0	1.43	38			
50	28.5	32.7	28.5	1.44				
				BEG 2445A (holotype)				
					44	3	7	17pr

TEXT-FIG. 3

a,h-j—Drakeoceras dellense, n. gen., n. sp. *a,h*, whorl sections at 40 and 75 mm. diam., and suture; UT 10103. *i*, whorl section of holotype at 75 mm. diam.; BEG 2445A. *j*, whorl section at 75 mm. diam.; BEG 3043B. All ×1.

b,c,e,n—Drakeoceras gabrielense, n. gen., n. sp. *b*, whorl section at 50 mm. diam.; UT 10127. *c,n*, whorl sections at 25 and 50 mm. diam., and suture; BEG 3043A. *e*, whorl section of holotype at 100 mm. diam.; UT 10121. All ×1.

d,f,g,m,o—Drakeoceras drakei, n. gen., n. sp. *d*, whorl section at 55 mm. diam.; UT 14446A. *f*, suture; BEG 20250, from the Weno formation, Bell Co., Texas. *g,m*, holotype, suture and whorl sections at 50 and 90 mm. diam.; BEG 20249. *o*, whorl sections at 60 and 100 mm. diam.; UT 1460. All ×1.

k,q—Drakeoceras lasswitzi, n. gen., n. sp. Whorl sections, ×1. *k*, at 50 and 95 mm. diam.; BEG 2391. *q*, at 60 and 125 mm. diam.; BEG 20251.

l—Drakeoceras maximum (Lasswitz, 1904), n. gen. Whorl sections of cast of holotype, ×1.

p—Drakeoceras, n. gen., n. sp. Whorl section, ×1, at 100 mm. diam.; BEG 2445B, Main Street formation, ½ mile S of Prairie Dell, Bell Co., Texas; collector: W. S. Adkins.

BEG 3043B appears to be transitional between *D. dellense*, n. sp., and *D. gabrielense*, n. sp.

Observations.—*Drakeoceras dellense*, n. sp., appears to have evolved from *D. gabrielense*, n. sp., perhaps by the caenogenetic development of the adult ornamentation of *D. dellense*, and these two species do occur together, although *D. gabrielense* appears earlier. Such forms as BEG 3043B (Text-fig. 3j and Pl. 10, fig. 10) seem to be transitional from *D. gabrielense* to *D. dellense*. *D. dellense* has a higher H/W ratio, the whorls remaining high to more advanced growth stages, and the species is more densicostate than any other Texas species of *Drakeoceras*. None of the other species of this genus possess intercalated ribs at or near mid flank.

Horizon and localities.—*Drakeoceras dellense*, n. sp., is known only from the lower part of the *Turrilites brazosensis* zone of the Georgetown formation and its equivalents. It occurs with *T. brazosensis* Römer, *Durnovarites adkinsi*, n. sp., *Drakeoceras gabrielense* n. sp., *D. drakei*, n. sp., and a new species of *Stoliczkaia*. *D. dellense* has been collected in Bell, Williamson, and Travis counties, Texas.

DRAKEOCERAS DRAKEI, n. sp.
Pl. 3, fig. 2; Pl. 4, fig. 1; Pl. 6, fig. 1–4; Pl. 10, fig. 1,2,6,8; Text-fig. 1e,3d,f,g,m,o

Holotype.—BEG 20249, deposited in the Bureau of Economic Geology, The University of Texas, Austin, Texas. It is from 10 to 15 feet below the top of the Georgetown limestone, 2 miles east of Belton, Bell County, Texas, and was collected by N. F. Drake, probably in 1892.

Specific characters.—Oligogyral, concentrumbilicate, sublatumbilicate, gradumbilicate, carinate. The whorl section is quadrate to subquadrate, and the H/W ratio is nearly always close to unity. Costae are relatively straight, appearing to turn adorad on the venter; rectiradiate, becoming markedly prosiradiate on the last third of the body whorl, as in most Mortoniceratinae (Pl. 6, fig. 3). Costation also becomes less robust on the orad part of the body whorl. Rib density in *D. drakei* ranges from 24 to 28 costae per volution at a diameter of 50 mm.; most of these are bifurcating. At a diameter of 100 mm. the rib density ranges from 28 to 31, and nearly all ribs are alternating, single, primary and secondary. One individual retains the aperture (Pl. 6, fig. 3,4). The rostrum is very short, and forms an angle of about 20 degrees with the periphery of the whorl. The diameter of this shell was about 120 mm. at the aperture.

BEG 20250 is septate to a shell diameter of about 67 mm., and the last two septa are closer together than are septa immediately preceding. The holotype (BEG 20249) is septate to 80 mm., with part of the body chamber present, and BEG 2445B is septate to 75 mm., with part of the body chamber present.

The sutures are not well preserved, as is usual in specimens preserved in carbonate rock, but the ventral lobe is narrow, the first lateral saddle is wide with the subsidiary lobe displaced asymmetrically dorsad; the first lateral lobe is well developed, and the second lateral lobe is reduced. In *D. dellense*, n. sp., in which the whorl section is much higher, the lateral saddles and lobes are not widened, if anything narrower, but the additional flank width results in a more complete development of the second lateral saddle.

UT 14446A has been included in *D. drakei*, n. sp., but it is atypical, apparently transitional to *D. georgetownense*, n. sp., and in UT 1460, although like *D. drakei* in the adult, the young appears to be transitional to the juvenile form of *D. gabrielensis*, n. sp.

Observations.—There is considerable variation in *Drakeoceras drakei*, n. sp., particularly in the elevation of the ventral element of the paired shoulder tubercle, as in UT 1460 and BEG 20249 (Text-fig. 3m,o; Pl. 10, fig. 2,6). UT 1460, as observed in whorl section at a diameter of 60 mm., seems to be evolving toward *D. gabrielense*, n. sp., and both this specimen and UT 14446A appear to have the ventral part of the outer whorl compressed. This is typical of both older and younger species of the genus, but not of the holotype of *D. drakei*. In these individuals the compression may be the result of compaction of sediments. There appear to be forms, such as UT 1460, transitional to *D. gabrielense*, n. sp., and forms, such as UT 14446A, transitional to *D. georgetownense*, n. sp. Consequently, al-

				Measurements				
				BEG 20249				
				(holotype)				
100	37.0	35.0	34.0	1.03	29	9	10	5pr
75	35.5	37.0	37.5	0.98	30	5	7	9pr
50	36.0	39.0	38.0	1.03	28	0	2	13pr
				UT 1460				
122	37.0	34.0			29	9	4	8pr
100	34.0	37.0	35.0	1.06	33	3	4	13pr
75	28.5	40.5	36.5	1.11				
60	30.0	42.5	36.5	1.16				
				BEG 20250				
100	35.5	35.0	34.0	1.03	26	10	6	5pr
75	36.0	38.5	38.0	1.04				
				BEG 2451				
100	36.5	34.0	33.0	1.03	31	12	13	3pr
75	36.0	37.5	37.5	1.00	30	6	6	9pr
50	32.0	40.0	38.0	1.05				
				UT 14446A				
86					28	7	9	6pr
75	40.5	33.5	34.5	0.96	27	1	4	11pr
60	38.5	35.0	35.0	1.00	26	1	3	11pr
50	39.0	37.0	38.0	0.97	24	0	4	10pr
40	42.5	40.0	44.0	0.92				

though UT 1460 has a whorl section and costation of *D. drakei*, the termination of the ribs on the venter and the juvenile whorl section more closely resemble those of *D. gabrielense*. Likewise UT 14446A has a slightly coarser costation, thus approaching *D. georgetownense*, but not sufficiently to be included in that species.

Horizon and localities.—*Drakeoceras drakei*, n. sp., is fairly abundant at some localities. The species ranges from somewhere in the *Mortoniceras wintoni* zone up into the lower part of the zone of *Turrilites brazosensis*. Probably that sequence of rocks between the zone of *Mortoniceras wintoni* (in abundance) and the zone of *Turrilites brazosensis* should be designated the *Drakeoceras drakei* zone. The specimens in the collections are mostly from Williamson and Bell Counties, Texas.

DRAKEOCERAS GEORGETOWNENSE, n. sp.
Pl. 8, fig. 1; Pl. 9, fig. 3; Text-fig. 1a

Holotype.—UT 863, from the middle part of the Georgetown limestone, on Smith's Branch, 1 mile east of Georgetown, Williamson County, zone of *Drakeoceras lasswitzi*, n. sp.

Specific characters.—Oligogyral, concentrumbilicate, gradumbilicate, sublatumbilicate, carinate. The whorl section is subquadrate, but the width is greater than the height at all diameters of more than 50 mm. H/W is 0.90 more or less at a diameter of 75 mm. UT 873 is septate to 90 mm. and the holotype is septate to 92 mm., the body chamber being small as the more adoral costae are swinging adorad on the apertural end of the shell, becoming extremely prosiradiate as is typical in the apertural parts of the body chambers of many Mortoniceratinae.

Costae are slightly rursiradiate on all visible whorls except the body chamber, and costae on the visible whorls of the holotype are coarse, paucicostate, ranging from 24 to 26 ribs per volution at diameters of 75 to 100 mm. Both shoulder elements are clavate, the dorsal element more so than the ventral element. The ventral element rises to an elevation at least equal to the elevation of the keel and maybe higher than the keel.

			Measurements					
			UT 873					
124	28.0	30.0			27	13	8	3pr
75	32.5	36.5						
			UT 863 (holotype)					
112 (maximum)								
100	40.0	35.0			26	8	8	5pr
75	36.5	36.0	39.5	0.92	25	1	4	10pr
60	34.0	36.0	38.0	0.98				

Observations.—The middle Georgetown limestone forms constituting *Drakeoceras georgetownense*, n. sp., are more paucicostate than the younger species of the genus such as *D. gabrielense*, n. sp., *D. dellense*, n. sp., and *D. drakei*, n. sp. The number of costae per volution may not be significantly different from that of *D. lasswitzi*, n. sp., but the costae are flexiradiate in the latter species and are prosiradiate rather than slightly rursiradiate. Also *D. georgetownense* has a smaller H/W ratio than any other recorded species of the genus, and it is more paucicostate at diameters of 50 mm and less.

Horizon and localities.—Drakeoceras goergetownense, n. sp., has been collected in the Georgetown limestone in Travis and Williamson Counties, Texas, from the zone of *Drakeoceras lasswitzi*, n. sp.

DRAKEOCERAS LASSWITZI, n. sp.
Pl. 5, fig. 5; Pl. 8, fig. 3; Pl. 9, fig. 7;
Text-fig. 2k,3k

Holotype.—BEG 18769, from the top of the Fort Worth formation, Rock Creek, east of Blum, Hill County, Texas, from the zone of *Drakeoceras lasswitzi*, n. sp.

Specific characters.—Oligogyral, concentrumbilicate, sublatumbilicate, gradumbilicate, carinate; whorl section slightly higher than wide in the adult, tapering very gently ventrad. Costae are not dense, ranging from 27 to 30 ribs per volution at a diameter of 100 mm. Costae are slightly prosiradiate and very slightly flexiradiate, recalling the ribbing of *Goodhallites*. Costae are bifurcating except on the body chamber, where they are single and alternating, primary and secondary, the primary costae bearing pronounced umbilical tubercles and all costae bearing the double shoulder tubercle. The mid flank of the rib may swell, but hardly becomes a tubercle. The umbilical tubercle is nodate to slightly bullate, and the elements of the shoulder tubercle are clavate.

BEG 2391 is septate to 87 mm., which is the maximum diameter of the mold. BEG 18769 is septate to at least 86 mm., and BEG 20251 is septate to 92 mm. BEG 20251 is nearly complete, since the ribs become markedly prosiradiate at the apertural end. BEG 2391 has most of the body chamber destroyed. The overlap of one whorl over the preceding extends to just cover the dorsal element of the shoulder tubercle.

(*See Measurements on page 29*)

Observations.—Drakeoceras lasswitzi, n. sp., like *D. kummeli*, n. sp., differs from other species of the genus in retaining the goodhallitine appearance into the adult stages. In *D. kummeli* the ribs are more flexiradiate, less pronounced at mid flank, and the tubercles and papillae are a little sharper. *D. kummeli* is probably the direct progenitor of *D. lasswitzi*. The H/W ratio is greater in the former than in the latter. In both of these species the pronounced bifurcation at the umbilical tubercle does not continue

EXPLANATION OF PLATE 9

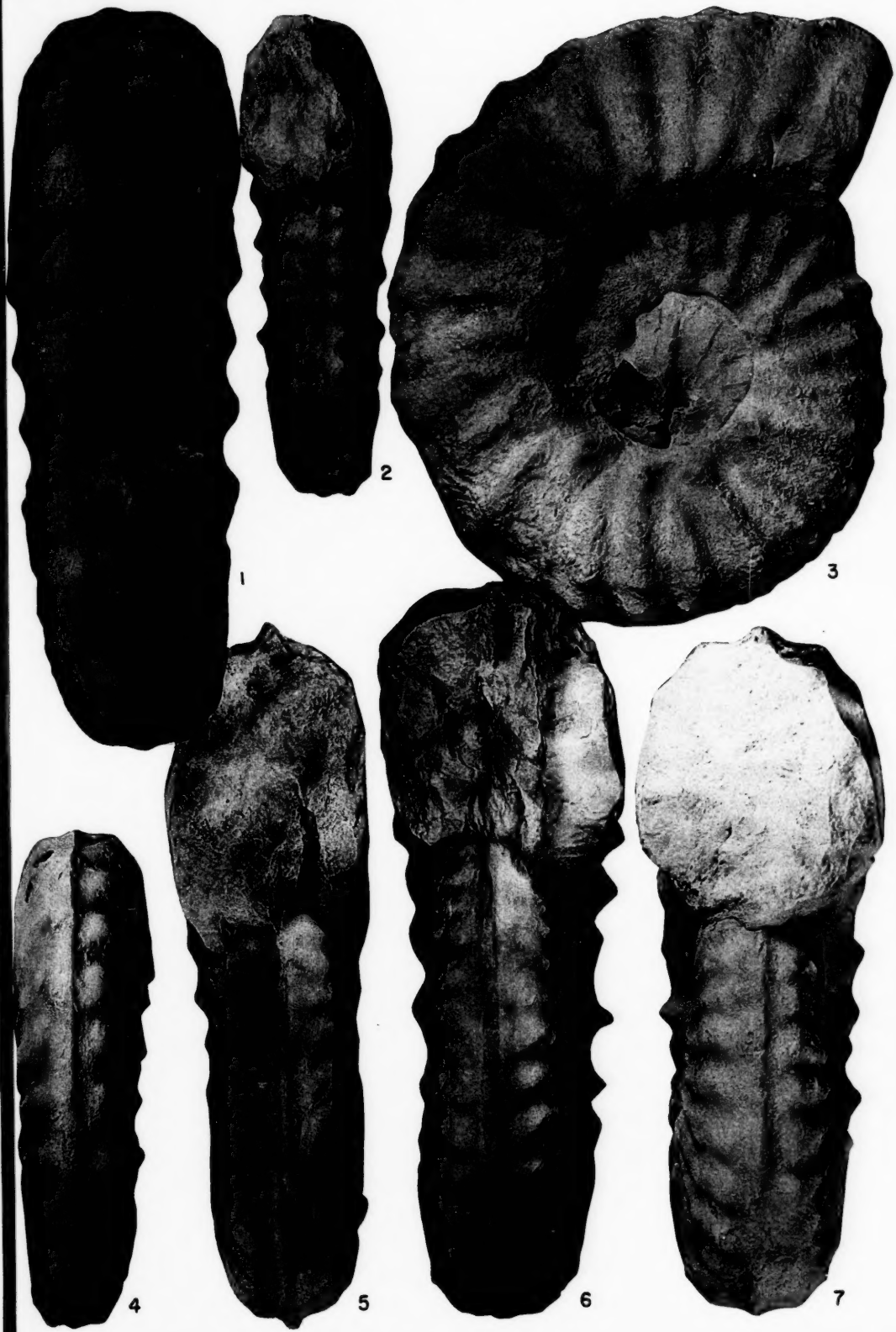
FIG. *1,6—Drakeoceras maximum* (Lasswitz, 1904), n. gen. Ventral views of cast of holotype, ×½. (p. 29)

2,4—Drakeoceras arringtoni, n. gen., n. sp. Ventral views of holotype, ×½; UT 10523. (p. 30)

3—Drakeoceras georgetownense, n. gen., n. sp. Ventral view of holotype, ×1; UT 863. (p. 27)

5—Drakeoceras kummeli, n. gen., n. sp. Ventral view of holotype, ×1; BEG 18727. (p. 21)

7—Drakeoceras lasswitzi, n. gen., n. sp. Ventral view, ×1; BEG 20251; collected from Bell Co., Texas, but horizon not designated. (p. 28)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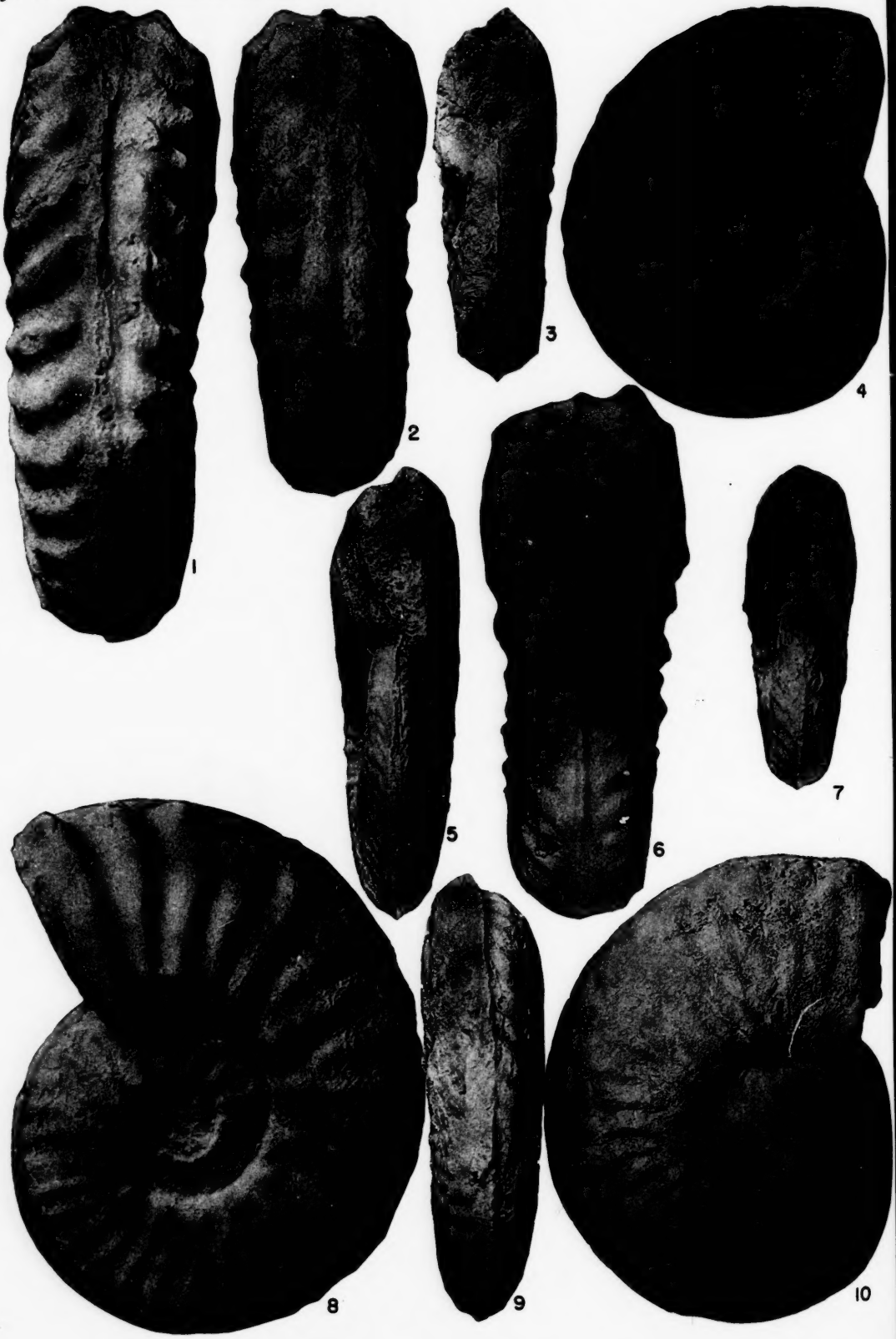
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Measurements

			BEG 18769 (holotype)					
100	35.0	38.5			27	2	3	11pr
75	32.0	38.5	35.5	1.09	29	1	2	13pr
50	32.0	38.0	36.0	1.06	27	1	2	12pr
			BEG 2391					
100	35.0	37.0	33.5	1.11	27	4	9	7pr
75	33.5	38.5	37.5	1.03				
50	35.0	42.0	42.0	1.00				
			BEG 20251					
134	35.5	33.5	31.5	1.06	29	12	11	3pr
100	34.0	38.0	35.0	1.08	30	5	7	9pr
75	33.5	41.5	37.5	1.10				

into the greater diameters (more than 100 mm) as in *D. maximum* (Lasswitz), and the costae do not have the marked prosiradiate flexure just ventrad of the umbilical tubercle that is so typical of *D. arringtoni*, n. sp. *D. arringtoni* and *D. maximum* are much larger species than any of the other species of the genus herein described.

Horizon and localities.—*Drakeoceras lasswitzi*, n. sp., is known from Williamson, Bell, and Hill Counties, Texas. It ranges down a few feet into the zone of *Drakeoceras maximum* (Lasswitz) and ranges upward for some interval, which, as yet, is not known to overlap the range of *Mortoniceras wintoni*. At the present time it is proposed to call that interval between the zones of *Drakeoceras maximum* and *Mortoniceras wintoni* the zone of *Drakeoceras lasswitzi*.

DRAKEOCERAS MAXIMUM (Lasswitz, 1904)

Pl. 3, fig. 4; Pl. 9, fig. 1,6; Text-fig. 31

Schloenbachia leonensis var. *maxima* LASSWITZ, 1904, Geol. and Pal. Abh., n. s. 6, pl. VI, fig. 2, text-fig. 5.

Pervinquieria maxima (Lasswitz). ADKINS, 1928, Univ. Texas Bull. 2838, p. 231 (pro parte), Pl. XIII, fig. 3.

Pervinquieria maxima (Lasswitz). ADKINS, 1933, Univ. Texas Bull. 3232, p. 363–371 (pro parte).

Holotype.—Adkins (1928) stated that the holotype was at the University of Breslau. A cast of the holotype is at the Bureau of Economic Geology, The University of Texas, Austin, Texas.

Specific characters.—Oligogyral, concentrumbilicate, gradumbilicate, sublatumbilicate, carinate; the whorl section is roughly subquadrate, tapering slightly ventrad, slightly higher than wide. The costation is moderately dense in the adult, with 32 ribs per volution at a diameter of 250 mm. in the holotype, increasing steadily and continually to 39 ribs per volution at a diameter of 100 mm. (rib density decreases with increasing diameter). Costae are very slightly prosiradiate to a diameter of 150 mm., rectiradiate on the body chamber, and the apertural part of the body whorl is absent on the holotype. The umbilical tubercle is pronounced and nodate to a diameter of 150 mm., becoming slightly bullate from that diameter on. The shoulder tubercles are more or less nodate at all diameters

EXPLANATION OF PLATE 10

FIG. *1,2,6,8*,—*Drakeoceras drakei*, n. gen., n. sp. *1*, ventral view, ×1; BEG 2451. *2,6,8*, lateral and ventral views of holotype ×1; BEG 20249, 10 to 15 feet below the top of the Main Street limestone, 2 mi. E of Belton, Bell Co.; collector: N. F. Drake, 1892. (p. 26)

3,7—*Drakeoceras gabrielense*, n. gen., n. sp. Ventral views of two juvenile specimens, ×1, *3*, BEG 3043A. *7*, UT 10127. (p. 22)

4,5,9,10—*Drakeoceras dellense*, n. gen., n. sp. *4,5,9*, lateral and ventral views, ×1; UT 10103, lower part of *Turrilites brazosensis* zone, Georgetown limestone, collected near Georgetown, Williamson Co., Texas, by Billy Walls, 1950. *10*, lateral view of individual transitional to *D. gabrielense*, n. sp., ×1; BEG 3043B, from Bell Co., horizon not designated. (p. 25)

beyond 100 mm., and at a diameter of 200 mm. the ventral element of the shoulder tubercle becomes relatively less pronounced. The rectiradiate ribs thicken slightly and are convex laterad, but not sufficiently so to be termed tuberculate. On the body whorl the costae and intercostae are about the same width; prior to the body whorl the intersoctae slightly exceed the costae in width. The mid-flank laterad thickening of the ribs is easily visible on the costal whorl section, and this thickening seems only to be the result of the non-nodate part of the rib parallelling the rounded flank of the intercostal section. Costae bifurcate to a diameter of 200 mm. more or less. The keel is pronounced, higher than adjacent tubercles.

Measurements of holotype

237	38.0	35.0	31.0	1.12	32	10	6	8pr
200	40.0	36.5	31.0	1.17	34	5	5	12pr
150	38.0	37.5	33.5	1.12	36	0	6	15pr
100	33.0	34.0			39	0	9	15pr
75	32.5							
60	34.0							
50	33.0							

Observations.—Many separate forms have been assigned to this species and the synonomy given by Adkins (1928) lists some forms which have a coarse, mortonicerine juvenile stage not found in the genus *Drakeoceras* (e.g., Bullard, 1925, pl. 22, fig. 1). The data listed above under specific characters is taken largely from the cast of the holotype to augment Lasswitz's (1904) description and the further remarks by Adkins (1928).

Unlike most of Lasswitz's illustrations his flank view of *D. maximum* (1904, pl. 6, fig. 2) is extremely misleading, but shows the essential bifurcation at the umbilical tubercle to an advanced stage. Adkins's (1928, pl. 13, fig. 3) shows the double shoulder tubercle as only an oblique photograph can.

D. maximum (Lasswitz) is larger than *D. kummeli*, n. sp., *D. lasswitzi*, n. sp., and *D. drakei*, n. sp. The young forms of *D. maximum* show strong bifurcation at the umbilical tubercles to diameters greater than the adults of the above species ever attain. *D. arringtoni* is very close to *D. maximum* as is an undescribed species of the genus which occurs with *D. arringtoni*. At a diameter of 150 mm. the whorl section of *D. arringtoni* is higher, and bifurcation does not continue to as large a diameter. The ventral element of the shoulder tubercle becomes higher in the adult stage of *D. arringtoni*, whereas in *D. maximum* it becomes lower and more obscure; *D. arringtoni* also has a sharp flexure in the ribs just ventrad of the umbilical tubercle which is not present in *D. maximum*.

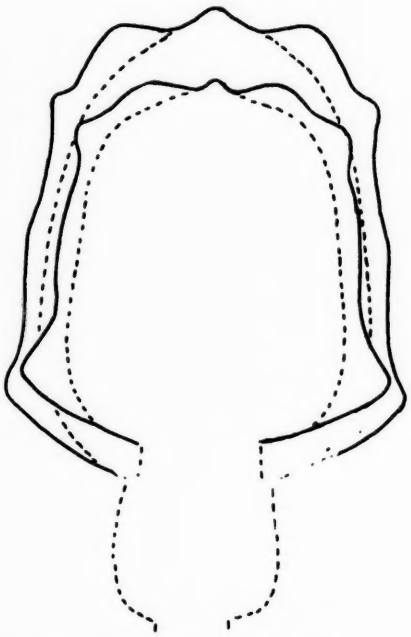
Horizon and locality.—According to Adkins (1933) the zone of *Drakeoceras maximum* (Lasswitz) occurs at a Fort Worth level above the zone of *Pervinquieria kiliani* (Lasswitz). Lasswitz's locality and age designation are in error as pointed out by Adkins (1928).

DRAKEOCERAS ARRINGTONI, n. sp.

Pl. 6, fig. 6; Pl. 9, fig. 2,4; Text-fig. 4

Holotype.—UT 10523, from low in the *Drakeoceras lasswitzi* zone, in an abandoned road metal pit on the Dedear Ranch, 0.3 mile east of U. S. highway 81, 3.0 miles north of the Brushy Creek bridge at Round Rock, Williamson County, Texas. Collector: D. E. Atchison, 1954.

Specific characters.—This species has all of the characters attributed to the genus. The whorl section is higher than wide, especially from a diameter of 100 mm. to greater diameters, and at a diameter of 150 mm. the H/W ratio is roughly 1.2. The flanks are slightly flattened, and the costal section shows a slight widening of the rib through mid flank, but not sufficiently to be called tuberculate. The flanks converge slightly ventrad. Costation changes from goodhallitine to adult at a diameter of about 90 mm., and the change is more gradual than in other Texas species of the genus. Costae are narrower than intercostae; only on the last whorl do the costae lose all flexuosity and become rectiradiate. Costae are flex-



TEXT-FIG. 4—*Drakeoceras arringtoni*, n. gen., n. sp. Whorl sections, ×1, at 120 and 150 mm. diam.; UT 10523.

iradiate in earlier stages with a sharp prosiradiate flexure just ventrad of the umbilical tubercle. On the body chamber costae are single, alternating primary and secondary, rectiradiate.

The umbilical tubercles are nodate to slightly bullate, the dorsal element of the shoulder tuberlce is faintly clavate, and the ventral element is nodate. The ventral element is low and rounded up to a diameter of about 120 mm. whereafter it becomes more pronounced and higher until, at a diameter of 150 mm. it is elevated almost to the height of the keel. The species is evolute, the dorsal element of the shoulder tubercle being visible on the inner whorls.

Observations.—Drakeoceras arringtoni, n. sp., differs from *D. maximum* (Lasswitz) in its sharp prosiradiate flexure just ventrad of the umbilical tubercle, in its higher whorl section beyond diameters of 120 mm., in the greater development of the ventral element of the shoulder tubercle beyond a 120 mm. diameter, in the disappearance of bifurcation at an earlier diameter, and in the dorsal elements of the shoulder tubercles being visible on the inner whorls when the outer whorls are in place. It differs from *D. kummeli*, n. sp., and *D. lasswitzi*, n. sp., in the greater involution of these two species, and in the low rounded ventral elements of the shoulder tubercles prior to a diameter of 120 mm. in *D. arringtoni*. *D. kummeli* and *D. lasswitzi* do not have the sharp prosiradiate flexure just ventrad of the umbilical tubercle which is so typical of *D. arringtoni*.

Horizon and locality.—Drakeoceras arringtoni, n. sp., is known only from the zone of *Drakeoceras lasswitzi*. It probably does not extend upward into the zone of *Mortoniceras wintoni*. The species is known only from Williamson County, Texas.

REFERENCES

ADAMS, BAXTER, 1953, Geology of southern Indio Mountains: Univ. Texas thesis.

ADKINS, W. S., 1920, The Weno and Pawpaw formations of the Texas Comanchean: Univ. Texas Bull. 1856, p. 1–172, 13 fig., 11 pl.

——, 1927, The geology and mineral resources of the Fort Stockton quadrangle: Univ. Texas Bull. 2738, 166 p., 8 figs., 6 pl.

——, 1928, Handbook of Texas Cretaceous fossils: Univ. Texas Bull. 2838, 385 p., 37 pl.

——, 1929, Some Upper Cretaceous Taylor ammonites from Texas: Univ. Texas Bull. 2901, p. 203–211, 2 pl.

——, 1931, Some Upper Cretaceous ammonites in western Texas: Univ. Texas Bull. 3101, p. 35–72, 2 fig., 4 pl.

——, 1933, The Mesozoic Systems in Texas, in Sellards, Adkins & Plummer, The Geology of Texas, vol. I, Stratigraphy: Univ. Texas Bull. 3232, p. 239–519, fig. 13–27.

Measurements of holotype

160					28	10	10	4pr
150	35.5	36.0	30.5	1.19	32	8	8	8pr
100	33.0	40.5	32.0	1.26	36	3	5	15pr
75	35.0	45.5	37.5	1.22	36	0	0	18pr
60	34.0	36.0						
50	34.0	35.0						
40	32.5	37.5						
30	33.5	43.5						

——, & ARICK, M. D., 1930, Geology of Bell County, Texas: Univ. Texas Bull. 3016, 92 p., 2 fig., 1 pl.

——, & WINTON, W. M., 1920, Paleontological correlation of the Fredericksburg and Washita formations in north Texas; Univ. Texas Bull. 1945, p. 1–128, 6 fig., 22 pl.

ALBRITTON, CLAUDE C., JR., 1937, Upper Jurassic and Lower Cretaceous ammonites of the Malone Mountains, Trans-Pecos Texas; Harvard Coll., Mus. Comp. Zool., Bull., vol. 80, no. 10, p. 391–412, pl. 1–9.

ALLDAY, E. C., 1953, Structure of southern Indio Mountains: Hudspeth County, Texas: Univ. of Texas thesis.

AMSBURY, D. L., 1957, Geology of Pinto Canyon, southern Presidio County, Texas, Univ. Texas dissertation.

ARRINGTON, R. N., 1954, Geology of the Berry Creek quadrangle, Williamson County, Texas; Univ. Texas thesis.

ATCHISON, D. E., 1954, Geology of the Brushy Creek quadrangle, Williamson County, Texas: Univ. Texas thesis.

BÖHM, J., 1910, L. Pervinquiere: Étude de Paléontologie Tunisiene, . . . , review of: Neues Jahrb. Band II, p. 149–155.

BÖSE, EMIL, 1910, Monografía geológica y paleontológica del Cerro de Muleros circa de cuidad Juárez, Estado de Chihuahua y descripción de la fauna Cretácea de la Encantada Placer de Guadalupe, Estado de Chihuahua, Mexico; Inst. Geol. Mexico, Bol., no. 25, 123 p., il.

——, 1923, Algunas faunas Cretacicas de Zacatecas, Durango, y Guerréro; Inst. Geol. Mexico, Bol., no. 42, 219+iv p., 19 pl.

——, 1928, Cretaceous ammonites from Texas and northern Mexico; Univ. Texas Bull. 2748, p. 143–312, 18 pl.

BOULE, M., LEMOINE, P., & THEVENIN, A., 1906–1907, Céphalopodes Crétáces des Environs de Diego-saurez, Part III, Paléontologie de Madagascar; Ann. Paléont., vol. 1, p. 173–192, pl. 14–20, vol. 2, p. 1–56, pl. 1–8.

BRAND, J. P., 1952, Cretaceous of Llano Estacado of Texas: Univ. Texas dissertation.

——, 1953, Cretaceous of Llano Estacado of Texas: Univ. Texas, Bur. Econ. Geol., Rept. Invest. no. 20, p. 1–59, 5 fig., 14 pl.

BULLARD, F. M., 1925, Geology of Love County, Oklahoma; Okla. Geol. Surv. Bull. 33, 77 p., 1 fig., 29 pl.

CONRAD, T. A., 1857, Description of Cretaceous and Tertiary fossils, *in* Emory, W. H., Report on the United States and Mexican Boundary Survey . . . : U. S. 34th Cong., 1st Sess., Senate Ex. Doc. 108, vol. 20 and House Exec. Doc. 135, vol. 14, vol. 1, pt. 2, p. 141–174.

CRAGIN, F. W., 1893, A contribution to the invertebrate paleontology of the Texas Cretaceous; Texas Geol. Surv., Ann. Rept. 4, pt. 2, p. 141–294, pl. 24–46.

DOUVILLÉ, HENRI, 1911, Évolution et classification des Pulchelliidés, Soc. geol. de France, Bull (4) 11, p. 285–320, 73 fig.

HAAS, OTTO, 1942, The Vernay Collection of Cretaceous (Albian) ammonites from Angola; Am. Mus. Nat. Hist., Bull., vol. 81, art. 1, p. 1–224, 2 tables, 33 fig., 47 pl.

——, 1955, Revision of the Jurassic ammonite fauna of Mount Hermon, Syria: Am. Mus. Nat. Hist., Bull., vol. 108, art. 1, 205 p., 30 pl.

HUMPHREY, W. E., 1949, Geology of the Sierra de los Muertos area, Mexico with description of Aptian cephalopods from the La Peña formation, Geol. Soc. Am. Bull., vol. 60, p. 89–176, 2 fig., 18 pl.

HYATT, ALPHEUS, 1903, edited by T. W. Stanton, Pseudoceratites of the Cretaceous; U. S. Geol. Surv. Mon. 64, 352 p., 47 pl.

IMLAY, R. E., 1938, Ammonites of the Taraises formation of northern Mexico; Geol. Soc. Am. Bull., vol. 49, p. 539–602, 15 pl., 4 fig.

——, 1940, Neocomian fauna of northern Mexico: Geol. Soc. Am. Bull., vol. 51, p. 117–190, 21 pl., 7 fig.

JONES, T. S., 1938, Geology of Sierra de la Peña and paleontology of the Indidura formations, Coahuila, Mexico; Geol. Soc. Am. Bull., vol. 49, p. 69–150, 13 pl., 4 fig.

KOSSMAT, FRANZ, 1895–1898, Untersuchungen über die südindische Kreideformation; Beitr. Palaeont. Geol. Oest-Ung. IX (1895), p. 97–203, pl. 15–25, XI (1898) p. 1–46, 89–152, pl. 1–8, 14–19.

KUMMEL, B. J., & DECKER, JACK M., 1954, Lower Turonian ammonites from Texas and Mexico; Jour. Paleont., vol. 28, p. 310–319, pl. 30–33, fig. 1–10.

LASSWITZ, RUDOLF, 1904, Die Kreide ammoniten von Texas; Geol. und Pal. Abh., vol. 10 (n. s. 6), Heft 4, 40 p., il.

MCCARTHY, J. F., 1953, Cretaceous ammonites of the Shafter area, Presidio County, Texas: Univ. Texas thesis.

RENZ, H. H., 1936, Neue Cephalopoden aus der oberen Kreide vom Rio Grande del Norte (Mexico und Texas); Abh. der Schweiz. Paleont. Gesellschaft, Band 57, 16 p., 4 pl.

RÖMER, FERDINAND, 1852, Die Kreidebildungen von Texas und ihre organischen Einschlüsse: 100 p., il., Bonn, Adolph Marcus.

SCOTT, GAYLE, 1926, Études stratigraphiques et paléontologiques sur les terrains Crétacés du Texas; l'Univ. Grenoble, Travaux lab. Geol. Fac. sci., p. 77–298, 3, pl.

——, 1928, Ammonites of the genus *Dipoloceras*, and a new *Hamites* from the Texas Cretaceous; Jour. Paleont., vol. 2, p. 108–118, 1 fig., 2 pl.

——, 1941, Cephalopods from the Cretaceous Trinity group of the south-central United States; Univ. Texas Bull. 3945, p. 969–1106, pl. 55–68, fig. 138–179.

SHUMARD, B. F., 1853, Paleontology: description of the species of Carboniferous and Cretaceous collected, *in* Marcy, R. B., Exploration of the Red River of Louisiana, in the year 1852; U. S. 32nd Cong., 2nd Sess., Senate Exec. Doc. 54, vol. 8.

SPATH, L. F., 1921, On Cretaceous Cephalopoda from Zululand; Ann. South Africa Mus., vol. 12, p. 217–321. pl. 19–26.

——, 1922, On Cretaceous Ammonoidea from Angola, collected by J. W. Gregory; Royal Soc. Edinburgh, Trans., vol. 53, pt. 1, p. 91–160, 4 fig., 4 pl.

——, 1931, 1932, 1933, 1934, 1941, 1942, A Monograph of the Ammonoidea of the Gault; Paleontographical Soc., vol. 83–86, p. 313–496, fig. 103–173, pl. 31–56; vol. 95–96, p. 609–720, fig. 218–248, pl. 65–72, table 1–4.

——, 1927–1933, Revision of the Jurassic cephalopod fauna of Kachh (Cutch); Paleont. Indica, new ser., vol. 9, mem. 2 (in 6 pts.), vii+945 p., 130 pl.

STEPHENSON, L. W., 1945, Larger invertebrate fossils of the Woodbine formation (Cenomanian) of Texas: U. S. Geol. Survey Prof. Paper 242, 226 p., 8 fig., 59 pl.

STIELER, CARL, 1920, Ueber sogennante Mortoniceraten des Gault: Centralbl. f. Min., p. 345–352, 392–400, 9 text fig.

STOLICZKA, FERDINAND, 1861–1865, Ammonitidae, with Revision of the Nautilidae . . . *in* the Fossil Cephalopods of the Cretaceous Rocks of Southern India, Paleont. Indica (1,3) I, p. 41–216, I-xiii, pl. 26–94.

VAN HOEPEN, E. C. N., 1931, Die Krytfauna van Soeloeland. 2. Voorlopige bescrywing van enige soeloelandse ammoniete. 1. *Lophoceras*, *Rhytidoceras*, *Drepanoceras* en *Deiradoceras:* Paleont. Navorsing Nasionale Mus., Bloemfontein, Deel I, Twede Stuk, p. 39–54, fig. 1–14.

——, 1941–1951b, Die Gekielde Ammoniete van die Suid-Afrikaanse Gault. *I.* (1941) Dipoloceratidae, Cechenoceratidae en Drepanoceratidae, Deel 1, Derde Stuk, p. 55–90, fig. 1–55, pl. 8–19; *II.* (1942) Drepanoceratidae, Pervinquieridae, Arestoceratidae, Cainoceratidae; Deel 1, Vierde Stuk, p. 91–157, fig. 56–173; *III.* (1944) Pervinquieridae en Brancoceratidae, Deel 1, Vyfde Stuk, p. 159–198, pl. 20–26; *IV.* (1946a) Cechenoceratidae, Diplooceratidae, Drepanoceratidae, Arestoceratidae, Deel I, Sesde Stuk, p. 199–260, fig. 174–268; *V.* (1946b) Monophyletism or Polyphyletism in connection with Ammonites of the South African Gault, Deel I, Sewende Stuk, p. 261–271; *VI.* (1951a) The so-called old mouth-edges of the ammonite shell, Deel I, Agtste Stuk, p. 273–284, fig. 269–287; *VII.* (1951b) Pervinquieridae, Arestoceratidae, Cainoceratidae, Deel I, Negende Stuk, p. 285–344, fig. 288–442: Paleont. Navorsing Nasionale Mus., Bloemfontein.

WALLS, BILLY, 1950, Geology of the Bell Gin Quadrangle, Williamson County, Texas: Univ. Texas thesis.

WINTON, W. M., 1925, The geology of Denton County, Univ. Texas Bull. 2544, 86 p., 8 fig., 21 pl.

——, & ADKINS, W. S., 1920, The geology of Tarrant County: Univ. Texas Bull. 1931, 123 p., 6 fig., 6 pl., 2 maps.

WRIGHT, C. W., 1952, A classification of the Cretaceous ammonites: Jour. Paleont., vol. 26, p. 213–222, fig. 1,2.

——, 1955, Notes on Cretaceous Ammonites.—II. The phylogeny of the Desmoceratacеae and the Hoplitaceae: Ann. Mag. Nat. Hist. (ser. 12), vol. 8, no. 92, p. 561–575.

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A LOWER CARBONIFEROUS BRACHIOPOD-CORAL FAUNA FROM NEW SOUTH WALES

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ABSTRACT—The brachiopod-coral fauna from Watts, Babbinboon, a locality on an horizon high in the Lower Burindi Group of New South Wales, is described. The new genera *Werriea* (Orthotetacea), *Unispirifer* and *Ectochoristites* (Spiriferinae), *Asyrinxia* (Syringothyrinae) and *Balanoconcha* (Terebratulacea), together with several new species, are described. The species *Rhipidomella australis* (McCoy) and *Spirifer latus* McCoy are redescribed from topotype material. It is concluded that the age of the fauna is upper Tournaisian and that there are strong affinities with both the European and North American regions. New species described are (*indicates type species): *Werriea australis**, *Schuchertella pseudoseptata*, *Dictyoclostus simplex*, *D. paradoxus*, *Rhipidomella myosa*, *Ectochoristites wattsi**, *Brachythyris pseudovalis*, *Strophopleura anterosa*, *Balanoconcha elliptica**, *Pugnax minutus*, *Chonetes careyi*, *Rugosochonetes? werriensis*, *Eumetria? mona*, *Lithostrotion voiseyi*.

INTRODUCTION AND ACKNOWLEDGMENTS

THIS work has been undertaken as part of a plan to zone and correlate the Lower Burindi rocks of northern New South Wales, and to determine the palaeogeographical significance of the faunas. The most prolific fossil localities are usually near the top of the Group, and have been collected from now for over half a century. The present paper is concerned with the fauna from one of the better known of these localities viz. Watts, Babbinboon, (grid reference, 570–637 Attunga One Mile Military Sheet), from which material has been described previously by Benson & Dun (1920). It is situated at the northern end of the Werrie Basin, a structure capably mapped by Carey (1934, 1937).

In order to provide an adequate basis for comparative work topotype and other material of *Rhipidomella australis* (McCoy) and *Spirifer latus* McCoy has been described. No material has been described from the type locality of these species, Lewinsbrook (grid reference, 608–882 Dungog One Mile Military Sheet), since the original work of McCoy in 1847.

I am indebted to Dr. Dorothy Hill for advice and for reading the manuscript; to Professor Alan Voisey for assistance in the field; to Drs. G. A. Cooper and A. Vandercammen for the gift of North American and Belgian specimens; to Drs. J. Selwyn Turner and D. Moore for the loan of chonetids from Yorkshire; to Mr. Harold Fletcher for the gift of photographs of type specimens in the Australian Museum, and to Professor O. M. B. Bulman for the gift of photographs of specimens in McCoy's collection housed in the Sedgwick Museum, Cambridge.

STRATIGRAPHY

This locality is stratigraphically situated near the top of the Lower Burindi Group. No accurate measurement has been made of the stratigraphic interval between it and the base of the Lower Kuttung Group, but it would be of the order of 100 feet. Below it in this region Carey (1934) has measured approximately 2500 feet of mudstone with interbedded oolitic limestones and sandstones of the Lower Burindi Group, all of which are, as I hope to show in a subsequent publication, of Tournaisian age. The only fossiliferous marine beds in the overlying Lower Kuttung Group are the coralline limestones at Babbinboon, the fauna of which has been described by Hill (1934), who suggested that it could be correlated with the Viséan D_2 zone of the British Isles.

The fossiliferous deposit itself is on a flat-topped knoll which has been completely isolated by erosion. The fossiliferous beds are well-bedded siltstones approximately 30 feet thick, and they are underlain by the greenish black mudstones typical of the Lower Burindi Group. It is difficult to determine the exact horizon within the deposit from which many of the specimens are

derived since a number of them has been collected from the loose fragments which cover the hillside. Nevertheless, it is apparent that certain beds are much richer in specimens than others and that while some species are found throughout the deposit, others tend to occur in abundance on one horizon only. For example, the coral *Caninophyllum* occurs in profusion in a bed about 1 foot thick near the top of the section and *Werriea* has been recovered only from the lowest fossiliferous beds. Most of the specimens have been derived from a bed approximately 6 feet thick near the middle of the section in which the larger genera of brachiopods occur in great abundance.

The section is capped by an oolitic limestone at present 8–10 feet thick, from which only a few specimens have been recovered.

ECOLOGY

The following observations give some indication of the depositional conditions prevailing during the formation of this deposit, and the environment inhabited by the organisms preserved in it.

1. About 300 yards to the south the oolitic limestone outcrops and is underlain by silty beds which are physically similar to those at the fossil locality but are palaeontologically barren. This silty-phase has not been recorded further to the south by Carey, and it thus appears to be a local development only. The form of the deposit cannot be determined due to the effects of erosion.

2. The matrix is clastic and of silt size. Angular fragments of quartz and feldspar in almost equal proportions make up approximately 80% of the clastic material in the rock. Clastic calcite is also an important constituent. Both brown and green biotite occur, the latter being much distorted, and minor quantities of epidote, muscovite and augite are also present. The matrix is very fine grained and contains abundant chlorite. The indications are, therefore, that this sediment accumulated below the zone of wave action.

The overlying oolitic limestone is composed almost completely of oolites set in a calcareous matrix. Quartz and rock fragments make up less than 5% of the rock.

3. Embedded in the silts at some points are numerous pieces of black shale many of which reach a length of 1 inch and a thickness of $\frac{1}{8}$ inch. There is no doubt that they indicate contemporaneous erosion of the surrounding Lower Burindi mudstones.

4. Delicate organisms such as fenestrate Bryozoa are rare.

5. The valves of most of the species of brachiopods are usually found dissociated but there are some species represented by an abnormally high percentage of specimens with associated valves; for example approximately 60% of the specimens of *Balanoconcha elliptica*, n. sp., are associated valves compared with 5%–10% of most other species.

6. In all of the specimens examined in which both valves were in position, the infilling matrix was the same as the external matrix. This suggests that the organisms concerned were alive when they reached the area of their final burial, although there is a slight probability that they may have died elsewhere and the shells were held together by the undecayed muscle fibres for a sufficient time to enable currents to sweep them to the area of burial.

7. Although the majority of specimens are isolated valves the fine details of structure and ornament are invariably in an excellent state or preservation. Even in such genera as *Echinoconchus* and *Waagenoconcha* the delicate spines are found to be still associated with the shells even though the preserving matrix is too coarse in most cases to permit the determination of their arrangement on the shell surface. The coarse elongate spines of *Dictyoclostus simplex*, n. sp., which may be up to 3 inches long have been found in position on numerous shells, but large numbers of them have been found lying unattached throughout the deposit. Transportation of shells belonging to these genera by current or wave action would result in the rapid removal of the spines so that the above observations suggest that they lived either in or marginal to the area in which they were buried.

8. It is common to find both juveniles and adults of species of all sizes occurring together in the one bed. The sorting action of the currents involved in the accumulation of the deposit was not strong. This is

weighty evidence in support of the suggestion that most of the species inhabited the area in which they are preserved.

9. The fossils particularly in the middle horizons of the deposit have no semblance of regular arrangement but are in a jumbled mass.

10. Woody fragments of small dimensions have been found on several horizons.

11. The solitary coral *Caninophyllum* which occurs in profusion on a horizon at the top of the sandy phase usually has worn dissepimentaria indicating wear by water.

All the available evidence suggests that the fossiliferous sediments were deposited in shallow water on a local topographical high the surface of which was however below wave base most of the time. That a shore line was possibly not far distant may be indicated by the presence of the oolitic phase and confirmed by the abundance of woody fragments throughout the deposit. Wave or strong current action is ruled out by the lack of sorting of the fossil material but the environment was sufficiently turbulent to prevent the establishment of delicate organisms.

On this silty eminence lived a fauna much richer than that of the surrounding mudstones. After death the skeletons of the animals were tumbled about and frequently bivalved forms were dissociated, but within a very short period they were completely buried. During the later periods of deposition when the surface of deposition was near wave base longer periods elapsed between death and burial and this accounts for the worn appearance of the solitary corals in the upper beds.

Brachiopods are generally considered to be epifaunal organisms, with the possible exception of some productids. A large number of the forms found in the Babbinboon fauna require a hard bottom to serve as a basis of pedicle attachment, (e.g., the Dalmanellacea, Spiriferacea and Terebratulacea) while others, such as the Orthotetacea, must have a suitable substratum for cementation. A substratum of silts with pieces of soft shale and occasional pebbles, such as constitute the bulk of the sediment throughout this deposit provides no suitable bottom for a large attached brachiopod fauna.

Productids, which are supported by spines, could have inhabited the silty bottom, but the attached forms could become abundant only when the shelly remains of organisms, which had previously inhabited the area, or which had been washed in from nearby areas, became sufficiently abundant to form a hard bottom, suitable for the attachment of pedicles or for cementation.

This is supported by the distribution of the various types of genera through the deposit. Among the earliest genera are *Echinoconchus* and *Waagenoconcha*, the latter frequently being associated with *Werriea*, and probably serving as a basis for its attachment, though there is no direct evidence for this. *Echinoconchus* occurs in great profusion in a grey silty sandstone together with a few dictyoclostids and orthotetids. It is only in the middle parts of the silty portion of the deposit that the attached species become abundant, and here they are associated with large accumulations of *Dictyoclostus*. It is possible that the influx of this latter genus provided a bottom sufficiently hard for brachiopods attached by a pedicle to become established, and once established the accumulation of their skeletal remains would ensure the continued suitability of the bottom for further generations until some outside factor forced their migration.

Of the other invertebrate groups only lamellibranchs and gastropods occur in sufficient numbers to affect the nature of the bottom, but neither of these groups occurs in large numbers in association with brachiopods. Gastropods, mainly *Loxonema* and related genera, occur in abundance on one horizon in which a few dielasmids are the only brachiopods. A pterioid is the only lamellibranch occurring in quantity, but since it was probably infaunal it would not have added much hard material to the bottom except perhaps as remains from dead individuals.

THE AGE OF THE FAUNA

Previous work.—Benson (appendix to Benson & Dun, 1920) in a comprehensive analysis of the fauna of the Burindi Group as a whole came to the conclusion (by an invalid technique) that a Lower Viséan age was indicated. The species which he considered were from horizons distributed through

some 4–5000 feet of sediment, and his comparative work was vitiated by the extremely uneven quality of the specific identifications available at that time. Similar views are adhered to in Benson & Smith (1923, p. 160) where it is claimed that

> the affinities of the majority of the species are with Eurasiatic types, showing very little in common with the Carboniferous faunas of America . . . ; no characteristic Tournaisian forms have been found. The whole fauna, indeed seems to be of Viséan age, and the Burindi Series should, therefore, be referred to the higher parts of the Lower Carboniferous.

Schuchert (1928) reviewing the work of Benson, states that "most of the brachiopods are of lower Avonian or Burlington = Keokuk kinds, and [I] would therefore make the age Osagean or Middle Mississippian . . . ." This statement is based upon the identifications used by Benson, though a more critical approach is adopted, and it fails to take into account the broad time interval occupied by Burindi rocks.

In 1934 and 1937 Carey recognized several fossil horizons in the Lower Burindi Group of the Babbinboon area, and sent to Delépine for examination a suite of goniatites from an horizon near the base of the Group, some 2000 feet stratigraphically below the horizon of the fauna herein described. Delépine (1941) correlated the goniatite fauna with that of the Vaulx and Calonne limestones of Belgium which are of Upper Tournaisian age. If this determination were correct the Babbinboon fauna here described ought to be well up in the Viséan.

The Bryozoa of the upper beds of the Lower Burindi Group at Clarencetown and Hilldale, which are approximately co-aeval with the Babbinboon beds, have been described by Crockford (1947, 1951), who correlates them with the "early part of the Osage Series of the United States and so to an horizon within the upper part of the Tournaisian".

Age of the Babbinboon fauna.—The features of the fauna suggesting an Upper Tournaisian age are: ***Unispirifer striatoconvoluta*** (Benson and Dun) which closely resembles the ***Spirifer tornacensis*** de Koninck group, which in almost all areas of outcrop characterizes the Middle and Upper Tournaisian; ***Tetracamera*** cf. ***T. subtrigona*** (Meek & Worthen) which is Upper Tournaisian in both North America and north east Kazakhstan, the only other areas where it has been recorded; ***Eumetria? mona***, n. sp., is closely comparable with ***Acambona prima*** White and ***Eumetria serpentina*** de Koninck which are typical Upper Tournaisian species in North America and Belgium respectively; ***Brachythyris pseudovalis***, n. sp., and ***Werriea australis***, n. sp., have as their nearest relatives ***B. suborbicularis*** Hall and ***O. keokuk*** Hall from the Upper Tournaisian of North America; ***Strophopleura anterosa***, n. sp., and ***Dictyoclostus simplex***, n. sp., are represented in the Upper Tournaisian Burlington limestone by ***Spirifer mundulus*** Rowley and ***Productus burlingtonensis*** Hall; ***Asyrinxia lata***, n. sp., may be related to ***Fusella nipponotrigonalis*** Minato from the Upper Tournaisian Jumonji beds of Japan, and if this is so it is the only record of this genus outside of Australia.

A slightly earlier age is suggested by the close affinity between ***Ectochoristites wattsi***, n. sp., and ***Spirifer gregeri*** Weller from the Chouteau limestone of the Mississippi valley.

Forms which suggest a Viséan age are: ***Echinoconchus gradatus***, n. sp., a species of the ***E. elegans***-type which is usually not found below the Viséan; ***Phricodothyris*** is not common below the Viséan overseas, but evidence from within New South Wales suggests that it descends almost to the base of the Tournaisian; ***Lithostrotion columnare*** Etheridge and forms of the ***L. stanvellense*** Etheridge-type had not previously been described outside of the Viséan in Eastern Australia; ***Caninophyllum sumphuens*** (Etheridge) is more closely related to certain Viséan varieties of ***C. archiaci*** than to the Tournaisian ***C. patulum***.

All of the other species are allied to overseas forms which range through the Dinantian and in some cases through the whole Carboniferous.

The weight of evidence from this study is thus strongly in favor of an Upper Tournaisian age, and supports the conclusions of Crockford (1951). It suggests that the age given by Delépine for the goniatites low in the Burindi is much too young, and as will be shown in a later study, this is supported

by a study of the brachiopods from horizons low in the Burindi Group.

AFFINITIES OF THE FAUNA

Western Europe.—The Upper Tournaisian of this province has many species in common with the Babbinboon fauna, but there are differences, which are due in part no doubt to general facies differences (George, 1952). *Schizophoria* cf. *S. resupinata* and *Leptaena* cf. *L. analoga* are common in New South Wales. *Rhipidomella australis* is very similar to some of the Tournaisian representatives of *R. michelini*, while *Unispirifer striatoconvolutus* is a near relative of *Spirifer tornacensis*. *Schuchertella pseudoseptata* has affinities with *S. wexfordensis* from the Tournaisian of Britain and Belgium and *Dictyoclostus simplex* resembles *D. vaughani* which is recorded from Britain, Belgium and Germany. *Eumetria serpentina* is a common Tournaisian species on the continent but its relationship to *E.? mona* cannot be determined because of a lack of information on the internal detail of the European species.

Punctospirifer is not common in the European Tournaisian and no species comparable with our *Punctospirifer* sp. have been observed. The genus *Phricodothyris* in Europe is distinguishable from the New South Wales species by its poorly developed dental lamellae, the absence of a median septum in the pedicle valve and the unplicated commissure, but it must be noted that in Britain at least, the genus does not occur below the Viséan and it is usually found only in the reef knoll facies. Echinoconchids of the *E. elegans*-type in this province are also restricted to the Viséan. *Ectochoristites* may be represented in the topmost Viséan or Namurian of Fifeshire.

One remarkable feature is the apparent absence of *Werriea* from the Dinantian rocks of Western Europe. Also absent are representatives of *Waagenoconcha*, *Asyrinxia*, *Balanoconcha* and *Tetracamera*.

Russia.—From the Donetz Basin Rotai (1931) has described an extensive fauna of Lower Carboniferous age. Many of his species, particularly those which are identified with Western European or American forms, are not figured, and it is difficult to gauge relationships from the descriptive remarks alone. Nevertheless the following species appear to have representatives in the funa herein described: *Pustula elegans* (similar to *Echinoconchus gradatus*) ranges from the Upper Tournaisian to the top of the Viséan; *Spirifer* spp. *tornacensis* (similar to *Unispirifer striatoconvoluta*) occurs in the Upper Tournaisian; *Squamularia lineata* (similar to *Phricodothyris triseptata*) ranges from the Upper Tournaisian to the Namurian. The bulk of the Babbinboon fauna however is not represented.

Sarycheva & Sokolskaya (1952) have summarized the stratigraphical paleontology of the Carboniferous Brachiopoda of the Moscow Basin. The Babbinboon fauna has several genera in common with these faunas but close specific comparison is not common. To judge from the figures, the *Schizophoria resupinata* is not similar to the species from Babbinboon. *Rhipidomella michelini*, ranging from the Viséan to the Upper Carboniferous is similar to *R. australis* and the Tournaisian *Leptaenella analoga* compares with the similarly identified form from Babbinboon. Externally, the three Viséan species *Schuchertella portlockiana*, *S. wexfordensis* and *S. radialis* compare with *S. psuedoseptata*, but no internals are figured. The only Dinantian *Orthotetes*, *O. hindi* from the Viséan, does not resemble *Werriea australis*. A Tournaisian species of *Waagenoconcha*, *W. krapivensis*, has been recorded, but in my opinion it would be more accurately referred to *Pustula*. There are no similar species of *Dictyoclostus*, but *Echinoconchus elegans* (Viséan to Moscovian) is similar to *E. gradatus*. The Tournaisian *Spirifer tornacensis* and the Viséan *Brachythyris ovalis* are represented. *Phyricodothyris lineata* is more closely related to the British than the Australian species, but the Lower Tournaisian *Punctospirifer malevkensis* is similar to *Punctospirifer* sp. So far as I am aware, no species of *Ectochoristites* or *Tetracamera* have been recorded from this area and the only species of *Eumetria* are not comparable with *E.? mona*.

Gorsky & Timofeeva (1939) have recorded from the Upper Tournaisian of the coal bearing series of the Kizel districts, Western Urals, several genera which have also been found at Babbinboon. The degree of relationship between the two faunas is difficult to assess because of a lack of figures,

but those species which may have representatives at Babbinboon are *Schizophoria resupinata, Orthotetes crenistria, Chonetes* aff. *C. papilionacea, Chonetes dalmaniana, Productus semireticulatus* var., *Pugnax ivanovi* and *Reticularia lineata.*

Tolmachoff (1924, 1926, 1931) has described the Lower Carboniferous fauna of the Kuznetsk basin. I have not seen his descriptive work, but it is possible that forms which he assigns to *Eumetria serpentina, Spirifer tornacensis, Leptaena analoga, Rhipidomella burlingtonensis, Schizophoria resupinata, Productus burlingtonensis, Reticularia lineata* and *Chonetes laguessiana* have representatives in the Babbinboon fauna.

Japan.—Hayasaka (1924) has described a fauna which includes forms of both Tournaisian and Viséan age from Omi-mura in Western Japan. The species referred to *Productus elegans* may be similar to *Echinoconchus gradatus* and *Reticularia lineata* is similar to *Phricodothyris triseptata* though the details of ornament of the Japanese species are still required in order to confirm this.

Minato (1951, 1952) has made known a poorly preserved Carboniferous fauna from the Kitakami Massif in the island of Honsyû. The fauna of the Upper Tournaisian Jumonji Stage has many species which are related to those herein described: *Orthotetes keokuk* resembles *Werriea australis; Spirifer kozuboensis* is close to *Unispirifer striatoconvolutus; Fusella nipponotrigonalis* may be related to *Asyrinxia lata;* and *Kitakamithyris semicircularis* is almost certainly closely comparable with *Phricodothyris uniplicata.* There is however a remarkable absence of dictyoclostids from the Jumonji Stage, and the distinctive *Eumetria, Tetracamera* and *Balanoconcha* are also wanting. The faunas from the other stratigraphic levels are not related to that herein described.

India.—Diener (1899, 1915) has described the faunas of the Upper Tournaisian *Syringothyris* limestones of Kashmir, Kanaur and Spiti. Of the species figured from Kashmir *Chonetes* cf. *C. kashmiriensis* is similar to *Chonetes careyi,* n. sp., and it is possible that *Spirifer* sp. ind. (cf. *S. bisulcatus* Sowerby) may be a species of *Unispirifer.* The Lipak fauna contains *Productus longispinus* which may be similar to *Dictyoclostus paradoxus,* n. sp., but insufficient details are available to be certain of this; *Chonetes lipakensis* Reed resembles *Chonetes careyi,* n. sp., the *Derbyia* cf. *D. senilis* is possibly a *Werriea* or an *Orthotetes* the figure given showing a structure like a small spondylium in the pedicle valve; the *Strophomena analoga* is unlike the form I have referred to *Leptaenella* cf. *L. analoga.*

China.—The Chinese Lower Carboniferous brachiopods are not well known. Ting (1931) has recorded many brachiopods from the Fengninian "System" but a large number of these are nomina nuda.

It is doubtful whether beds of Tournaisian age have yet been described from Yunnan. None of the species recorded from the Lower Carboniferous by Mansuy (1912) bear resemblance to the Babbinboon species. Reed (1927) has described a small fauna of Viséan age, which includes only two species, *Leptaena analoga* and *Spirifer tornacensis,* which have representatives in the Babbinboon fauna.

Tian-Shan.—The Lower Carboniferous faunas of this region have been described in a series of monographs by German and Russian authors (see Muir-Wood, 1948). The faunas so far described are of Viséan or Namurian age and the figured species show little relation to those described here.

United States of America.—In the Burlington and Keokuk limestones of the Mississippi Valley no less than fourteen brachiopod genera from New South Wales are represented by closely related species. *Leptaena* cf. *L. analoga* is represented by the same species; *Rhipidomella australis* by *R. burlingtonensis* and *R. myosa* by *R. diminutiva; Schizophoria* cf. *S. resupinata* is very similar to *S. swallovi; Werriea australis* and *Orthotetes keokuk* are related as also are *Dictyoclostus simplex* and *D. burlingtonensis.* Among the chonetids *Chonetes careyi* compares with *Chonetes illinoisensis.* The spiriferids include *Unispirifer striatoconvolutus* which is comparable with *Spirifer forbesi; Brachythyris psueodovalis* which is nearly related to *B. suborbicularis; Punctospirifer* sp. which may be similar to *P. subtextus* and *Strophopleura anterosa* which is close to *Spirifer mundulus. Eumetria? mona* is, so

far as can be ascertained, a relative of *Acambona prima*. *Camarotoechia* sp. is represented by *C. elegantula* and *Tetracamera subtrigona* is present.

In addition there are other related species in rocks of Lower Viséan and Lower Tournaisian age. *Echinoconchus gradatus* is similar to *E. biseriatus* and *Pugnax minutus* to *P. wortheni*, both from the Salem (Lower Viséan) limestone. *Ectochoristites wattsi* and *Spirifer gregeri* from the Chouteau (Lower Tournaisian) limestone are closely related.

The genus *Phricodothyris* is possibly directly related to *Torynifer* which is represented by *T. pseudolineata* in the Keokuk limestone. So far as I am aware there are no representatives of *Waagenoconcha*, *Asyrinxia* or *Balanoconcha* in the Dinantian of North America.

With respect to the corals, *Lithostrotion* has been found (Hill, 1948) but no *Caninophyllum* has yet been recorded.

Australia.—Faunas with many elements in common with that from Babbinboon have been found at many localities near the top of the Lower Burindi Group in northern New South Wales. In Queensland the only Upper Tournaisian fauna yet described, viz. that from Mt. Morgan (Maxwell, 1954), is rather small and is not closely comparable with the New South Wales material.

In summary then, the fauna contains a large percentage of cosmopolitan genera; *Balanoconcha* and possibly *Asyrinxia* are the only endemic forms; closest affinity appears to be with the Upper Tournaisian of the Mississippi Valley though this conclusion may well need modification as further faunas are described from New South Wales and South and East Asia.

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA

Superfamily STROPHOMENACEA Schuchert, 1896

Family STROPHOMENIDAE King, 1841

Genus LEPTAENELLA[1] Sokolskaya, 1952

Genotype: *Producta analoga* Phillips

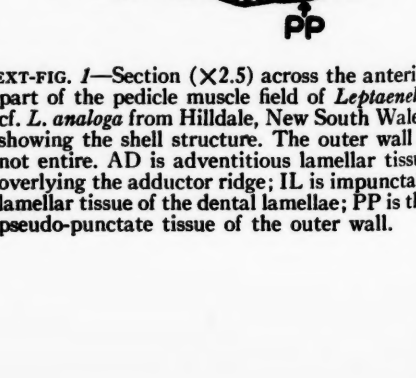
Diagnosis.—According to Sokolskaya (1954) this genus includes species which are similar in form and outline to *Leptaena* Dalman, but which differ from that genus in their larger size, the presence of a high marginal ridge on the interior of the brachial valve and the presence of a well-developed spondylium and adductor platform in the pedicle valve.

Remarks.—Sokolskaya based her studies on Russian specimens assigned to *L. analoga* (Phillips). Specimens from the Lower Burindi Group at Hilldale, New South Wales, which are very similar to *L. analoga*, have been sectioned, and show a spondylium formed in the manner described for the Russian specimens (see Text-fig. 1). The dental lamellae are supported on pseudopunctate shell material which sweeps up from the outer wall of the valve, but they themselves are quite impunctate.

Sections of the only Lower Paleozoic specimens available to me, *L. richmondensis* Foerste from the Waynesville Formation from Oxford, Ohio, (Upper Ordovician), show only a weak pseudospondylium formed by the thickening of the shell wall around the muscle field. This supports the evidence put forward by Sokolskaya based on a study of Russian material.

Further, though the New South Wales specimens of *L. analoga*-type all have a high keel-like marginal ridge in the brachial valve, in *L. richmondensis* (as in other American Lower Paleozoic species) this ridge is very poorly developed.

Thus, though examination of the genotypes of neither *Leptaena* nor *Leptaenella* has been possible, the evidence outlined above so confirms the observations made on the Russian material that these differ-



TEXT-FIG. 1—Section (×2.5) across the anterior part of the pedicle muscle field of *Leptaenella* cf. *L. analoga* from Hilldale, New South Wales, showing the shell structure. The outer wall is not entire. AD is adventitious lamellar tissue overlying the adductor ridge; IL is impunctate lamellar tissue of the dental lamellae; PP is the pseudo-punctate tissue of the outer wall.

[1] Since this paper went to press, Dr. Helen Muir-Wood has pointed out to me that *Leptaenella* Sokolskaya, 1952, is in fact an objective synonym of *Leptagonia* McCoy.

ences between the Carboniferous and Lower Paleozoic species formerly assigned to *Leptaena* appear to have much more than local significance. The genus *Leptaenella* Sokolskaya is therefore tentatively accepted as valid, pending the study of the genotypes.

Species which are probably assignable to *Leptaenella* were already developed in the Lower Devonian. That two distinct leptaenoid stocks were present at this time has long been recognized. For example, Caster (1939, p. 25) states

> There seem to have been at least two strains of leptaenoids in the Lower Devonian. Those of the Helderbergian are usually smaller and recall Silurian and even Ordovician representatives whereas the Oriskanian and Onondagan forms, as Nettelroth (1889, p. 150), and others have pointed out, are consistently larger, more flabellate and ventricose than the previous forms.

Such species as *L. rhomboidalis* var. *ventricosa* (Hall) from the Oriskanian of North America and *L. boyaca* Caster from a similar horizon in Colombia show the deep, cuspidate muscle attachment in the pedicle valve as is characteristic of *Leptaenella*. Though the true spondylioid nature of this structure cannot be determined without sectioning, its form is most suggestive of the *L. analoga* type. Hall's variety also shows a deep marginal ridge in the brachial valve, though *L. boyaca* according to Caster shows "no evidence of a diaphragmal callosity". Nevertheless his figure (1939, pl. 1, fig. 7) seems to show a marginal ridge on the right side which has been broken off the remainder of the specimen.

Range.—Lower Devonian to Lower Carboniferous.

LEPTAENELLA cf. L. ANALOGA (Phillips)
Pl. 13, fig. 20,21

Description.—Only two specimens have been found at Babbinboon, an external and internal mould of each valve.

Exterior: The pedicle valve is slightly convex toward the umbo, flattens out anteriorly and is geniculate at the edge of the visceral disc. The surface is crossed by about 20 closely set irregular concentric wrinkles, and fine costellae which number 12 or 13 per 5 mm. on the median anterior portion of the valve. The hinge line is by far the widest part of the shell and the ears are mucronate. The cardinal area is well developed and the delthyrium is partly (about half) covered by a strongly arched pseudodeltidium.

The brachial valve is gently convex across the visceral disc which is bounded anteriorly and laterally by a deep rounded depression which fits into the pedicle valve. Beyond this depression the valve is geniculate.

Interior: The muscle field is deeply cuspidate in form. The adductor scars are triangular in outline, situated on a sharply elevated platform and are divided by a slight but distinct sharp median keel. The diductors are longitudinally striated. There is a low rounded ridge swinging off from the hinge line at a distance of some 15 mm. from the umbo and separating the ears from the visceral disc. The pallial sinuses are not clearly outlined. The surface within a radius of 8 mm. from the limits of the muscle field, except for a small area in front of the adductor scars which apparently was occupied by the primary pallial trunks, is finely pustulose.

The cardinal process is directed at right angles into the pedicle valve and its inner surface is profoundly bifid. A short stout ridge runs laterally from each lobe of the cardinal process bounding the sockets. The slightly ellipsoidal posterior adductor scars are depressed posteriorly and elevated anteriorly. Their rear ends are separated by a triangular platform. Between their front portions are two small ovate eminences (visible on Pl. 3, fig. 20) which may be small secondary adductor scars. Anterior to this is a subtriangular region with a strongly elevated margin and a narrow excavated central portion which contains the anterior adductor scars. A very faint sharp median ridge divides these scars and is continued forward of the platform some 5 mm. A high keeled marginal ridge extends around the lateral and anterior portions of the visceral disc. The shell surface to each side of the muscle platform is finely but densely pustulose.

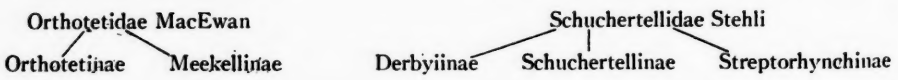
Remarks.—Populations of this genus from other localities are very variable in form and it is not safe to draw comparisons when only two specimens are available. However, in all observable characters, this form falls within the range of variation of *L. analoga* (Phillips) in the European area (e.g., see

Demanet, 1934, p. 61), where it ranges through the whole Dinantian.

Superfamily ORTHOTETACEA Williams, 1953

Williams included in the Orthotetacea four families: Orthotetidae MacEwan, 1939, Gemmellaroiidae Williams, 1953, Scacchinellidae Williams, 1953, and Thecospiridae Bittner, 1893; all except the first consist of only a few genera of a specialized type and are restricted to the Permian or Triassic. The Orthotetidae is subdivided into three subfamilies: Orthotetinae Waagen, 1884, characterized by the presence of dental lamellae; Schuchertellinae Williams, 1953, characterized by the loss of dental lamellae through obsolescence; and Davidsoniinae King, 1850, a small unusual Middle Devonian group without costellae. He does not name the genera which he would include in the Orthotetinae or the Schuchertellinae, but from the diagnoses and ranges given, the former is apparently intended to embrace *Orthotetes*, *Fardenia*, *Schellwienella*, *Meekella*, *Geyerella*, *Orthotetina* and *Orthotetella*; and the latter such genera as *Schuchertella*, *Streptorhynchus*, *Kiangsiella* and *Derbyia*. In its dependence on the presence or absence of dental lamellae as the most fundamental feature of taxonomic significance, this classification follows the pattern set by Girty (1908) and followed by almost all subsequent workers (e.g. Thomas, 1910; Dunbar & Condra, 1932). In my opinion (for reasons see later) the reduction and development of dental plates has taken place independently in several unrelated stocks at various times, and a classification based entirely on the presence or absence of these plates is necessarily unnatural.

Stehli (1954) has followed Williams in his basic approach to the subdivision of the group though his nomenclatorial reforms have been much more far reaching, as is shown in the diagram below.



Stelhi has also suggested a phylogeny in which the Orthotetidae and Schuchertellidae are shown as separating as early as the Silurian.

Dunbar & Condra (1932) presented an entirely different phylogenetic scheme in which three stocks were already distinct in the Silurian and develop independently until the Permian. According to these authors *Derbyia* developed from *Orthotetes*; the genera *Meekella* and *Geyerella* which are equipped with dental plates are unrelated to *Orthotetes*; and another lineage, without dental lamellae, includes *Schuchertella*, *Streptorhynchus* and *Kiangsiella*.

In any classification of the Orthotetacea the following points must be considered:

(1) *Schuchertella* is the basis of a relatively stable stock derived from the Silurian genus *Fardenia* (Williams 1951, p. 120), and ranging through to the Permian (Dunbar & Condra, 1932, p. 117; Stehli, 1954, p. 298). The Pennsylvanian genera *Derbyoides* Dunbar & Condra, and *Tapajotia* Dresser are much more closely related to the schuchertelloid stock than to *Derbyia* as their original authors suggested (see discussion below under *Schuchertella*).

(2) Though the genotypes of *Schuchertella* and *Orthotetes* are superficially dissimilar in size and contour, many species of *Schuchertella* approach *Orthotetes* in both of these characters (e.g., *S. rubra* Weller and *S. desiderata* Hall & Clarke). Further, the internal structure of the brachial valve is very similar in both genera, though that of the pedicle valve is quite distinct, *Orthotetes* having a spondylium formed by the union of the dental lamellae and *Schuchertella* lacking dental lamellae. Morphologically between these two genera, and in the correct stratigraphical position, stands the Lower Carboniferous genus *Werriea*, n. gen., in which short dental lamellae are buttressed against an independent median septum to form a spondylium. Some species of *Schuchertella* (see below) approach this structure with a low median plate dividing the muscle scars and buttressing the rudimentary thickenings along the inner edge of the del-

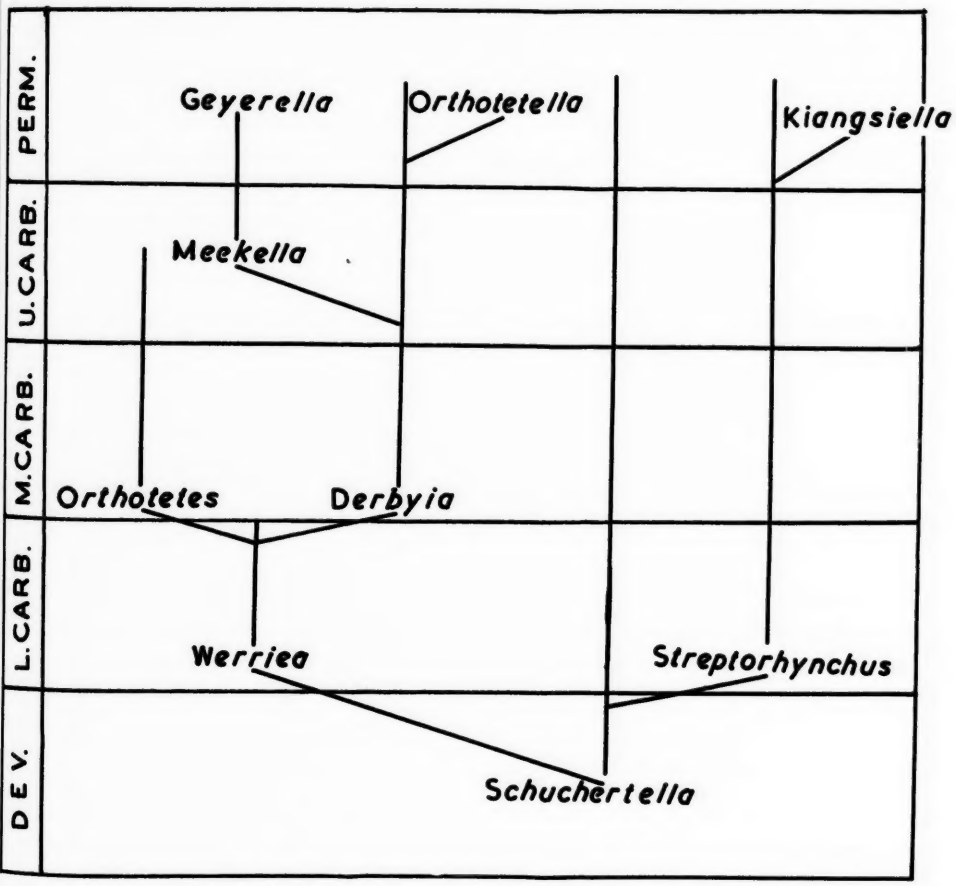
thyrium in the umbo, though a spondylium is never formed. It is possible, then, to trace a morphological series from *Schuchertella* through *Werriea* to *Orthotetes*.

(3) *Streptorhynchus* and allied forms with-

out dental lamellae or median septum in the pedicle valve, and with schuchertelloid dorsal cardinalia, were derived from the schuchertelloid stock in the Mississippian and form a continuous and apparently monophyletic line through to the Permian.

(4) The median septum in *Derbyia* appears to be formed by the union of the dental lamellae on the floor of the valve as in *Orthotetes*. The dorsal cardinalia however provide a clear basis of distinction since *Derbyia* has a high and distinctly constructed cardinal process, very long crural plates which project out into the valve and short buttress plates bounding the sockets. *Orthotetes* has a dorsal cardinalia fundamentally similar to *Schuchertella*. A search of the literature indicates that the earliest true *Derbyia* is probably *D. gigantea* Thomas from the Millstone Grit of Britain, and true *Orthotetes* dates from approximately the same time in Russia and elsewhere (Sarycheva & Sokolskaya, 1952). The origin of the derbyioid dorsal cardinalia is obscure. It is possible that *Orthotetes* and *Derbyia* represent distinct stocks which evolved from *Werriea* in late Namurian time. Alternatively *Derbyia* may have been derived from *Schellwienella* in Namurian times. Only the former alternative is shown in the accompanying figure.

(5) The derbyioid dorsal cardinalia is found only in the Middle and Upper Carboniferous and Permian genera *Derbyia*, *Orthotetella*, *Meekella* and *Geyerella*. *Orthotetella*, in which the spondylium homeo-



TEXT-FIG. 2—A possible phylogeny of some genera of the Orthotetacea. An alternative arrangement with regard to *Derbyia* is suggested in the text.

morphs that of *Orthotetes*, could be derived from *Derbyia* by the rapid evolution of the dental lamellae in Permian times, and *Geyerella* was undoubtedly developed from *Meekella* by the union of the dental lamellae on the floor of the valve.

At the present stage of our knowledge I think it unsafe to press the erection of new taxonomic units above generic rank in this superfamily. For most workers such units are necessarily derived from phylogenetic considerations, which at present are in a very fluid state. Hence in the accompanying tentative phylogenetic sequence, which embodies the points outlined above, genera have been used as pegs on which to hang the scheme.

Genus WERRIEA, n. gen.

Orthotetes Fischer de Waldheim, WELLER, 1914, Mon. Illinois State Geol. Surv., p. 74–78, pl. 6, fig. 1–14, pl. 7, fig. 1–4.

Genotype: *Werriea australis*, n. sp.

Diagnosis.—This genus includes orthotetids in which the greatest width is at or near the hinge. The profile of the pedicle valve is flat or resupinate and the brachial valve strongly convex. The cardinal area of the pedicle valve is moderately high and bears the usual surface ornament of the family, and the brachial area is narrow. Both valves are costate, the costae increasing by intercalation. Thick, but short, dental lamellae unite with an independent median septum to isolate a small triangular spondylium. The cardinal process is a short thick structure which bears a variable median ridge on its antero-ventral surface and is quadrilobed on its posterior surface. surface. The crural plates are short, simple and subparallel to the hinge.

Remarks.—Thomas (1910, p. 101) has reviewed opinions expressed to that date concerning the nature of the relations of the dental lamellae to the median septum in *Orthotetes*. In his view the median septum in this genus is "due to the fusion of the dental plates on the floor of the valve", and "this fused part has extended forward as a single plate." He quotes Girty however as believing that the median septum and dental lamellae are independent structures.

Recently the Russian material of the genotype of *Orthotetes*, *O. radiata* (Fischer), has been redescribed by Sarycheva & Sokolskaya (1952) and Sokolskaya (1954). In this latter work it has been shown that the short spondylium, regarded by most authors as the most significant character in the diagnosis of *Orthotetes*, may be present only during the early stages of ontogeny, the later stages having the spondylium filled with shelly matter. Because of this Sokolskaya considers this feature to be of minor taxonomic importance, and places *Derbyia* Waagen as a synonym of *Orthotetes* Fischer. This is unsatisfactory since, as has already been pointed out, *Derbyia* and *Orthotetes* are clearly distinguishable on the basis of the structure of the cardinal process, crural plates and buttress plates.

In her generic diagnosis of *Orthotetes*, Sokolskaya (1954, p. 137) states that in young specimens the dental plates are united in front and are together prolonged into a median septum, and her fig. 54 clearly illustrates this, thus supporting the conclusions of Thomas outlined above.

In the specimens from Babbinboon herein assigned to *Werriea*, n. gen., there is no doubt that the dental lamellae and the median septum are completely independent structures, and that the spondylium is formed by the dental lamellae butting against the septum near its apex. This condition is found also in the American Lower Carboniferous species *Orthotetes keokuk* (Hall) and *Orthotetes kaskaskiensis* (McChesney), as is well shown by the descriptions of Weller (1914). Of the former species he states (p. 76) that "the dental plates usually join the median septum near the beak to form a shallow triangular chamber in the apex of the valve" and (p. 77) he has observed one specimen in which "the dental plate is joined with the median septum on one side but not on the other." In the latter species the dental plates are reduced but they are (p. 78) "sometimes slightly extended anteriorly and join with the median septum to form a shallow triangular chamber." In this species which is younger than *O. keokuk* the inconstancy of the development of the spondylium seems to indicate a secondary reduction of the dental lamellae towards the *Schuchertella* stage.

Range.—Lower Carboniferous in Aus-

tralia and America though this may well be extended geographically by critical study of the Lower Carboniferous species commonly referred to *Orthotetes*.

WERRIEA AUSTRALIS, n. sp.
Pl. 11, fig. 1–7

Holotype.—F. 2545, University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The adults are large. The pedicle valve is semicircular in outline, the greatest width being at or just in front of the hinge. Its profile is flat or more frequently slightly resupinate. Growth is not regular and all stages are marked by broad irregularly developed concentric folds. The umbo is high, convex, and obtuse, and may be distorted. The cardinal area is of moderate height and is either flat or gently convex. The surface differentiation of the area has not been observed but this may be due to poor preservation. A highly arched pseudodeltidium completely covers the delthyrium, the edges of which diverge at an angle of approximately 45°. The ornament consists of narrow, sharply elevated costae separated by broader, flat interspaces. In large specimens four orders of costae are present. The primary costae are almost uniform in size. Those of new orders are very small when first introduced but gradually attain the size of previous orders and subsequently remain uniform. The spaces between the costae carry one or two fine striae. Growth lines are inconspicuous.

The brachial valve is strongly and evenly convex with slightly flattened auriculations which merge imperceptibly into the body of the valve. The umbo is broad and convex and the cardinal area very narrow. The ornament, so far as can be ascertained from the material available is similar to that of the pedicle valve.

Interior: The dental lamellae in adults are thickened structures which unite with the median septum isolating a small spondylium which in adults varies in length from two to four millimetres. The median septum is deep and extends approximately one quarter of the length of the valve. Its shape varies with age: in the youngest specimens it is almost linear while in the largest adult it is strongly wedge-shaped. It never reaches to the anterior edge of the muscle field. The muscle scars are broad and flabellate, and are continuous into the umbo. In length and width they are between one third and one quarter of the length and width of the valve respectively. Their outlines are poorly defined and it is not possible to distinguish between adductors and diductors.

The cardinal process is a thick squat structure which projects abruptly into the pedicle umbo. On its antero-ventral surface is a low rounded median ridge of very variable strength. Its extremity is broadly bifid. A deep median groove divides its posterior surface, and each half is further subdivided by another groove of smaller size.

Short heavy crural plates curve laterally from the base of the cardinal process at an angle of some 30° to the hinge line. Proximally these plates are recurved to meet the hinge line and thus completely enclose the apex of the sockets for a very short distance. Distally they become free and spoon shaped and their edges sharpen to form the crural bases. A faint rounded median ridge which is not continuous with the cardinal process divides the indistinct adductor scars.

Dimensions (mm.).—

Pedicle Valve

Length	Width	Length of median septum	Length of muscle field	Width of muscle field
52	90	15	16	22
40	60	—	—	—
40	60	11	—	—
42	62	11	—	14
41	63	10	—	—
—	62	10	9	—

Remarks.—There is a remarkable resemblance between this species and *O. keokuk* (Hall) from the Keokuk limestone of the Mississippi valley. In this latter form however the hinge line is relatively shorter and the muscle field is situated much further forward in the pedicle valve than in *W. australis*, n. sp.

No species referable to *Werriea* have been recorded from the Lower Carboniferous of western Europe.

Genus SCHUCHERTELLA Girty
Genotype: *Streptorhynchus lens* White

Diagnosis.—These are biconvex, planoconvex or slightly resupinate shells of small to medium size, in which the greatest width is at or near the hinge. The cardinal area is never high and is ornamentally divided in the manner normal for the superfamily. The surface of both valves is costate, the costal pattern being very variable. The teeth are supported on low ridges which border the margins of the delthyrium. There is usually no median septum in the pedicle valve, but in some species a very weak and variable plate may be present. The cardinal process is bifid at its tip and is deeply divided medially on its posterior surface, each half being further subdivided by the muscular facet. The crural plates are short and comparatively slender and are recurved forming deep spoon-shaped sockets. When present, the median ridge in the brachial valve is low and rounded.

Remarks.—The presence of a low median septum in the pedicle valve of species closely allied in other respects to the genotype of *Schuchertella* has long been recognized, even though it has never been noted in the genotype itself. Hall, for example, in 1867 (p. 68) described in *Streptorhynchus pandora* Billings from the Devonian of New York, "a short low mesial septum in the upper part"; and Thomas (1910, p. 101) has pointed out that the specimen figured by Davidson (1857, pl. 26, fig. 5) as *Streptorhynchus crenistria* Phillips, is in fact a *Schuchertella*. More recently Cooper (1944, pl. 132, fig. 46) has figured a specimen of *Schuchertella desiderata* (Hall & Clarke) in which there is a small callist in the umbo of the pedicle valve giving rise to three short plates in the manner described below in *S. pseudoseptata*, n. sp. Stainbrook also has observed a septum, since in a generic diagnosis (1945, p. 34) he states that a "slight median ridge generally divides the muscle scars."

That such a median plate is not of generic value can be shown by its extreme variability, e.g., within the population of *S. pseudoseptata*, n. sp.

Because of the inordinate emphasis placed by most workers on the internal structures of the pedicle valve many Lower Carboniferous species allied to *Schuchertella*, but bearing a median plate in the pedicle valve, have been erroneously referred to *Derbyia*. The most distinctive features of *Derbyia* are the

> strong and widely diverging crural plates, which extend with increasing height well out into the shell as septum-like ridges bounding the sides of the muscle scars. [Dunbar & Condra, 1932, p. 76]

These plates are buttressed to the hinge by subsidiary plates. So far as I am aware these structures have not been described in any Dinantian species referred to *Derbyia*. Demanet (1934, p. 90) has referred *D. depressa* to *Derbyia* on the basis of "une lame mince, très délicate, qui se brise souvent et qu'il est toujours très difficile de mettre en évidence." However the crural plates, although not illustrated, are described as "courtes et epaisses," a description which scarcely suggests similarity to *Derbyia*.

From the Zone d'Etroeungt, Gallwitz (1932, p. 99–100) has described as *Derbyia kayseri* a form in which a tolerably strong median septum, 4 mm. long in a shell of total length 50 mm.), is developed. It does not reach to the umbo but stops 2 mm. from it. The crural plates are short and merely bound the dental sockets. There is no real evidence of derbyioid affinities.

The genus *Derbyoides* Dunbar & Condra from the Pennsylvanian of Nebraska, which has a median septum which is "rather weak and low, extending not over one third the distance to the front of the valve," and cruralia comparable with *Schuchertella*, was probably derived from a schuchertelloid rather than a derbyioid stock. Similar remarks apply to the genus *Tapajotia* Dresser which is probably a synonym of *Derbyoides*. It is interesting to note that the specimens figured by Davidson (1857, pl. 26 and fig. 5 and 6) which were referred by Thomas (1910) to *Schuchertella* are said by Dresser (1954, p. 37) to belong to *Tapajotia*.

Range.—The genus ranges from the Lower Devonian to the Permian, and is world wide in its distribution.

SCHUCHERTELLA PSEUDOSEPTATA, n. sp.
Pl. 11, fig. 8–13

Holotype.—F. 2560. University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The adult shell is larger than the genotype. The greatest width is at or near the hinge and the outline is almost semicircular. The umbo of the pedicle valve is convex but as a whole the valve is flattened or slightly resupinate. The cardinal area is of moderate height and is either flat or gently convex. The delthyrial angle approximates to 55°, and the delthyrium is completely covered by the highly arched pseudodeltidium. The radial ornament is of two types; the costae are narrow and sharply elevated being separated by broad flat-bottomed depressions. They increase by intercalation and on the largest specimens costae of four orders are present. Between the costae two to four striae are present.

Ribs of all orders tend to attain the same size although in some specimens the primary costae may remain slightly larger than those of later orders. There are eight to eleven costae per 5 mm. on the median portion of the valve 20 mm. from the umbo. On a specimen 30 mm. long there are approximately 100 costae around the margin of the valve.

The brachial valve is only slightly but evenly convex longitudinally and is almost elliptical in outline. The dorsum is gently flattened or bears a faint depression from the umbo to the anterior margin. The umbo is flat and obtuse. A very narrow cardinal area is present. The ornament is similar to that of the pedicle valve.

Interior: The dental supports are reduced to ridges bounding the inner margins of the delthyrium. Within the apex of the umbo a small callist is occasionally developed, and in those specimens in which it occurs a short sharp median ridge 2 to 3 mm. long, and two much shorter subparallel lateral ridges, are derived from it. It is thought that these latter ridges bound the posterior margins of the adductor scars. In a specimen 30 mm. long the edge of the median ridge is only 5 mm. from the tip of the umbo. Specimens without a callist have a simple median ridge or none at all. The muscle scars are not distinguishable.

The cardinal process is a low broad structure. Its antero-ventral face is broadly convex and is divided by a broad low median boss, and its tip is pronouncedly bilobed. The posterior surface bears a deep median groove which broadens toward the tip, and each half of the process is then further subdivided by subsidiary grooves. The base of the cardinal process is produced laterally into the crural plates which proximally are completely recurved to meet the inner edge of the cardinal margin, thus completely enclosing the sockets. This enclosed section is short, and distally the edges of the sockets are broadly open and the tips of the socket plates are produced into short bluntly pointed crural bases. The bases of the socket plates lie parallel to the hinge line. A very low rounded median ridge which arises anterior to the cardinal process divides the poorly defined adductor scars.

Dimensions (mm.).—

Pedicle valve

Length	Width	Length of median septum
30	38	3
23	36	0
23	31	3½
21	—	3—

Remarks.—Certain specimens referred by Demanet (1934, pl. 9, fig. 4–9) to *S. wexfordensis* Smyth compare closely with the present species in size and form and the cardinalia of the brachial valve, but the ornament is finer. *S. wexfordensis* in Belgium ranges from T_n2a to T_n3b.

The North American *Schuchertella rubra* Weller from the Fern Glen formation has much finer costae.

No other comparable species have been described.

Superfamily DALMANELLACEA Schuchert & Cooper, 1932

Family SCHIZOPHORIIDAE Schuchert & Cooper, 1932

Subfamily SCHIZOPHORIINAE Schuchert & Cooper, 1932

Genus SCHIZOPHORIA King, 1850

Genotype: *Conchyliolithus Anomites resupinatus* Martin, 1809

Remarks.—Schuchert & Cooper (1932, p. 143) have given an account and discussion of the morphology of the genus. These authors make no mention of the bifid nature of the posterior adductor scars in the

brachial valve such as have been described by George & Ponsford (1938, p. 244) in *S. nuda* George & Ponsford and *S. hudsoni* George. Scars of this type have been found in the species described herein as *S.* cf. *S. resupinata*, and indeed in all of the species of *Schizophoria* from the Carboniferous of New South Wales.

Range.—The genus ranges from the Silurian to the Permian. During Lower Carboniferous times it was cosmopolitan.

SCHIZOPHORIA cf. S. RESUPINATA (Martin)
Pl. 12, fig. 1–5

Orthis (*Schizophoria*) *resupinata* (Martin), BENSON & DUN, 1920, Proc. Linn. Soc. New South Wales, vol. 45, no. 179, p. 345, pl. 19, fig. 10,11.

Description.—Exterior: The shell is of medium size for the genus. The pedicle valve is variable in outline from ovate to subrectangular. In general it is convex, tending to flatten over the anterior half of the valve, though occasional individuals among the larger specimens are distinctly resupinate. The anterior of the valve bears a faint depression which develops into a flexure of variable height at the anterior margin. The well developed strongly apsacline cardinal area ranges in width from 0.5 to 0.6 of the total width of the valve. The surface of the cardinal area is slightly concave except immediately beneath the umbo, which is a little incurved. The delthyrial angle averages 65°. The cardinal extremities are well rounded. Fifteen to 16 costae occur in a breadth of 5 mm. at a distance of 2 cm. from the umbo. Spine bases are sparsely distributed.

The brachial valve is of variable convexity, the height averaging about one-third of the length of the valve. The umbo is small and obtuse. A small proportion of the specimens is rounded on the dorsum, but the majority bears a very shallow depression of variable width, which originates between 5 and 15 mm. anterior to the umbo. The anterior of the commissure is broadly plicate, and in forms with a well developed median depression, may be slightly sulciplicate.

Interior: The umbo of the pedicle valve is much thickened. The stout teeth are supported on short unthickened dental lamellae, from the anterior edges of which arise low angular ridges which completely encircle the muscle field. The diductor scars are broad and flabellate, comparatively flat, and occasionally bear broad faint radial ridges. The adductor ridge rises abruptly between the divaricators. It is triangular in section, its apex being either angular or slightly rounded (Text-fig. 3). The whole muscle field is slightly variable in proportion but is usually a little less wide than long. From the inner anterior extremity of each divaricator scar arises a primary pallial trunk which may be either straight or slightly convex inwards. These extend to within approximately 4 to 10 mm. of the anterior margin. They may develop large secondary sinuses laterally but most frequently they appear to be simple over most of their course and give rise to a series

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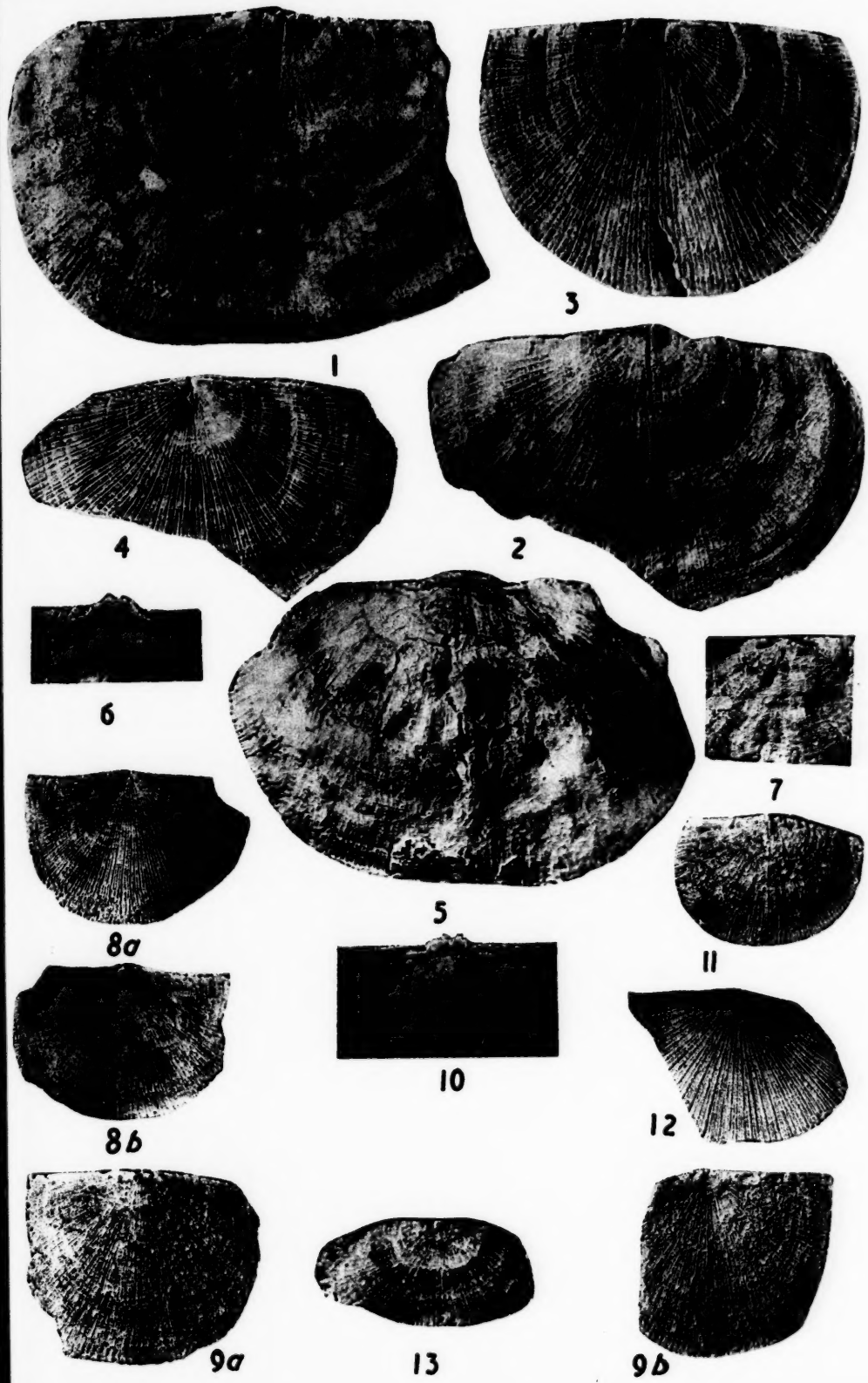
EXPLANATION OF PLATE 11

(All specimens from Watts, Babbinboon, and all specimens natural size unless otherwise stated. All specimen numbers refer to the University of New England Collections.)

FIG. *1–7*—*Werriea australis* n. gen., n. sp. *1*, holotype, mold of interior of pedicle valve; note the spondylioid structure, F. 2545A; *2*, mold of pedicle interior, F. 2540A; *3,4*, molds of two pedicle exteriors, F. 2853 and F. 2549B; *5*, mold of brachial interior, F. 2539; *6,7*, imperfect cast of a cardinal process, and mold of a cardinal region of two brachial valves, F. 2539 and F. 2851. (p. 45)

8–13—*Schuchertella pseudoseptata*, n. sp. *8a,b*, molds of the exterior and interior of a brachial valve, F. 2833–4; *9a,b*, holotype, molds of interior and exterior of a pedicle valve, F. 2560A,B; *10*, an imperfect cast of a cardinal process showing the median boss and the apex of the muscular facets. The cast does not show a sufficient depth for the crural plates as it is impossible to press the material into the deepest part of the mold; ×2, F. 2843; *11*, mold of a pedicle interior; the photograph gives a false impression of the depth of the septum which in fact is only 0.3 mm. high at its highest point, F. 2555B; *12*, mold of a pedicle exterior, F. 2835; *13*, mold of a pedicle interior showing the septal pattern, ×1.4, F. 2607. (p. 46)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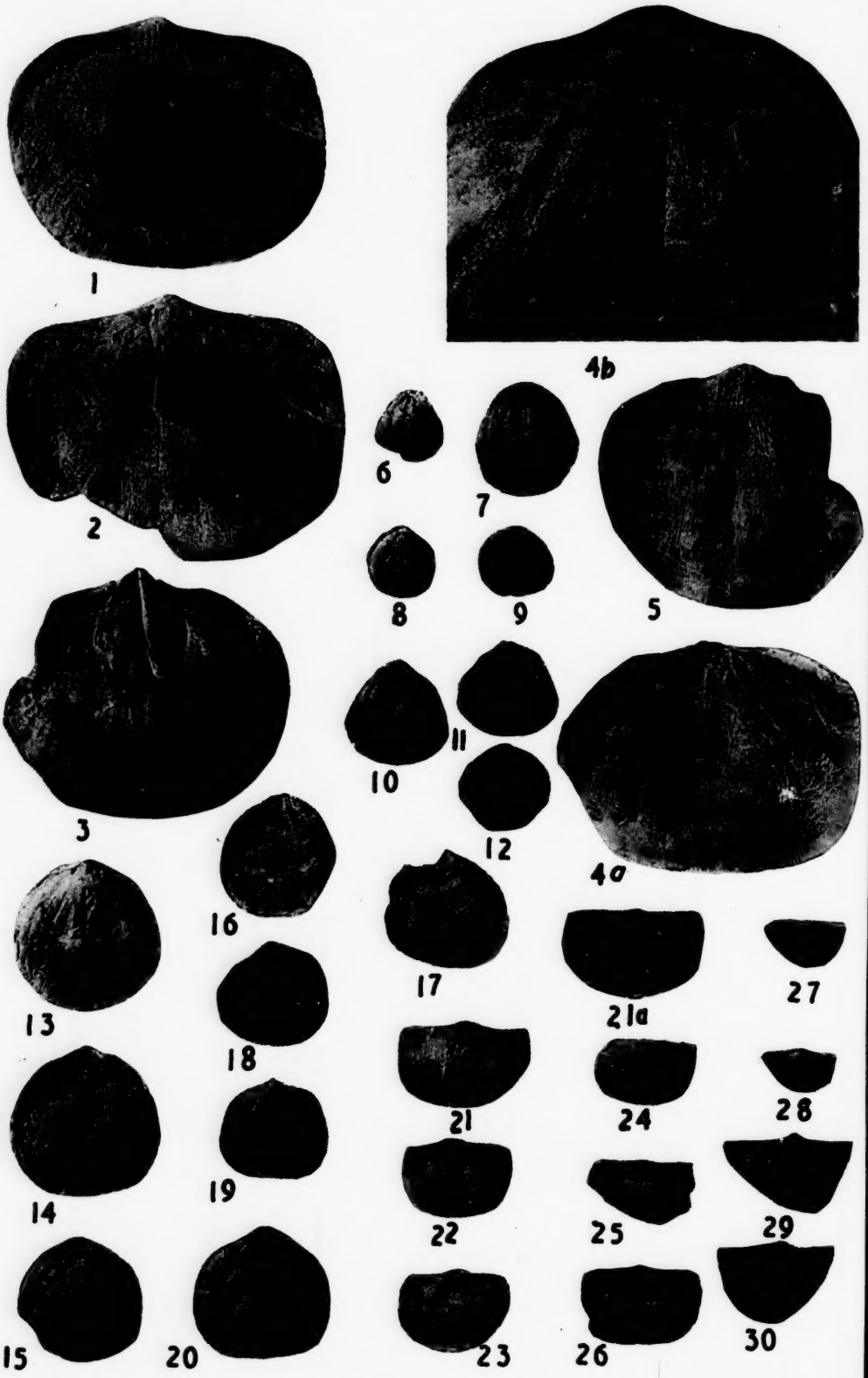
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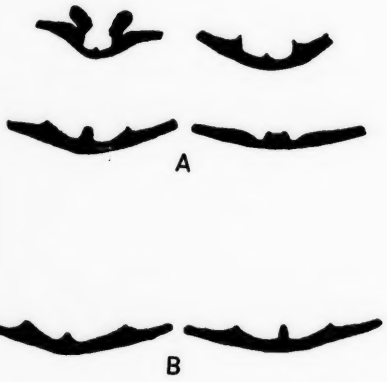
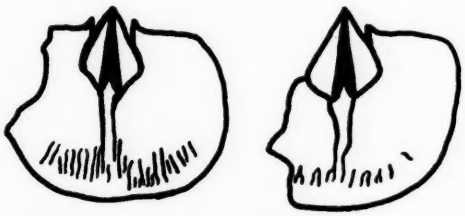


TEXT-FIG. 3—Sections through the pedicle valve of *S.* cf. *S. resupinata* to illustrate the form of the muscle field; *a*, Serial sections through a single specimen; *b*, sections showing variation in the shape of the adductor ridge. ×0.8.

of smaller and often indistinct sinuses which are arranged around the margin of the valve (Text-fig. 4).

The brachial valve is only slightly thickened in the umbo. The brachiophore plates are short (7 or 8 mm. long in a valve of total length 40 mm.), bluntly rounded and not recurved. The fulcral plates are very small, not completely enclosing the sockets. The cardinal process is formed of a strong median process flanked by up to five much smaller accessories on each side. The



TEXT-FIG. 4—Sketches of the pallial sinuses in the pedicle valves of *S.* cf. *S. resupinata*. ×$\frac{2}{3}$.

myophore on the median process is only slightly enlarged. The muscle field is enclosed by indistinct ridges which develop from the anterior edge of the brachiophore plates. In the centre of the field is a broad but very low platform which narrows anteriorly and bears a low median carina. The adductor scars consist of a large lacrimate anterior pair and a digitate postero-lateral pair. These latter scars may each be formed of a bifid single scar, the two branches of which are united at their anterior edges, or they may be formed of two quite separate scars. The pallial sinuses are very poorly defined in most specimens, but in one well preserved specimen there appear to be 6 primary trunks: two slightly diverging from the anterior edge of the median platform and one from each division of the posterior adductor scars (Text-fig. 5).

EXPLANATION OF PLATE 12

(All specimens natural size, from Watts, Babbinboon, and specimen numbers refer to the University of New England Collections unless otherwise stated.)

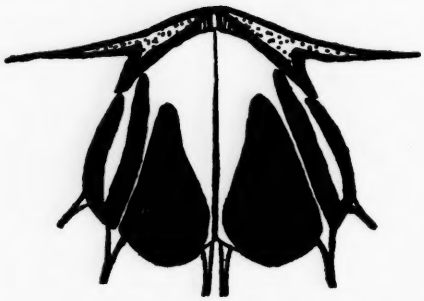
FIG. *1–5—Schizophoria* cf. *S. resupinata* (Martin). *1,2*, pedicle exteriors, F. 2804 and F. 1206; *3*, pedicle interior, F. 1166; *4a,b*, brachial interior, and enlarged view of the muscle field of the same specimen, F. 2805; *5*, brachial exterior, F. 1160. (p. 48)

6–12—Rhipidomella myosa, n. sp. *6,7*, molds of two brachial interiors, F. 2659 and F. 2617; *8*, mold of pedicle interior, F. 2645; *9*, cast of pedicle exterior, F. 2654; *10*, holotype, mold of pedicle interior, F. 2651; *11*, cast of pedicle exterior, F. 2897; *12*, brachial exterior, F. 2648. (p. 54)

13–20—Rhipidomella australis (McCoy). *13*, mold of a pedicle interior from Clarencetown, F. 2777; *14*, mold of a brachial exterior from Clarencetown, F. 2776; *16*, mold of a pedicle exterior of a topotype, F. 2779; *17*, mold of the pedicle interior of a specimen from Clarencetown, F. 2771; *18*, mold of the pedicle exterior of a paratype, E. 10662, Sedgwick Museum, Cambridge; *19*, lectotype, mold of a pedicle interior, E. 10663, Sedgwick Museum, Cambridge; *20*, mold of the pedicle interior of a topotype, F. 2783. (p. 52)

21–26—Chonetes careyi, n. sp. *21,21a*, casts of two pedicle exteriors. F. 2677 and F. 2889; *22*, holotype, mold of pedicle interior, F. 2666; *23*, mold of pedicle interior, F. 2672; *24*, mold of brachial exterior, F. 2665; *25,26*, casts of two brachial interiors, F. 2706 and F. 2675. (p. 63)

27–30—Rugosochonetes? werriensis, n. sp. *27*, mold of a pedicle interior, F. 2878; *28*, holotype, cast of pedicle exterior, F. 2869; *29,30*, casts of two brachial interiors, F. 2865, and F. 2880, both ×2. (p. 66)



TEXT-FIG. 5—Sketch showing the variation in the form of the adductor scars in the brachial valve of *S.* cf. *S. resupinata*. ×2.

Dimensions (mm.).—The dimensions of the pedicle valves are given in the accompanying scatter diagrams.

internal structures of *Schizophoria resupinata*, recent papers being concerned almost exclusively with the external form and ornament (Bond, 1951; Parkinson, 1954), though the former author also dealt with the angle of divergence of the dental lamellae. Work on the Australian species of the genus indicates that many internal features such as the form of the cardinal process, arrangement of the pallial sinuses and the proportion and form of the muscle scars of both valves provide a basis for specific distinction, and it is considered probable that the present interpretation of *S. resupinata* will require revision as detailed studies are made on these features in specimens from various horizons in Europe. In my opinion it is unsafe to base

Brachial valves

The "Total length of the muscle field" is measured from the base of the cardinal process to the anterior edge of the muscle field.

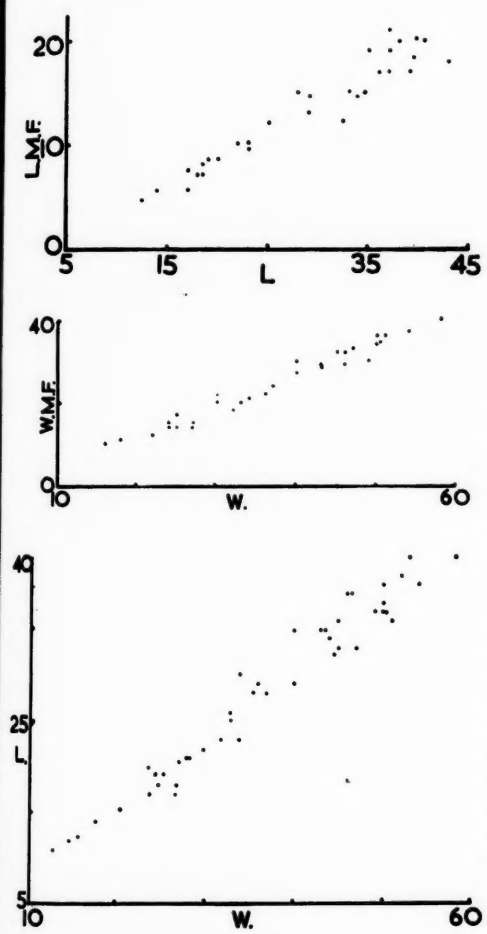
Length	Width	Height	Total length of muscle field	Total width of muscle field	Length of each anterior adductor scar	Width of each anterior adductor scar	Distance between outer limits of anterior adductor scars
39	48	13	—	—	—	—	—
38	48	14	—	—	—	—	—
38	50	15±	—	—	—	—	—
37±	—	13	15½	15½	—	—	—
36	48	12	14½	15	8½	—	11
36	46	14	—	—	—	—	—
36	46	14	15½	16½	11	5	14
36	45±	—	14	14½	—	4	10
27	33	8	13	11½	—	—	—
26	34±	7	10	11	—	—	—

Remarks.—Martin's species *Anomites resupinatus* was declared invalid by the International Commission on Zoological Nomenclature in 1948. Muir-Wood in 1951 made application to the Commission "that the trivial name *resupinatus* Martin, 1809, in its published form *Anomites resupinatus*, commonly known as *Schizophoria resupinata*, should be validated under the plenary powers." Herein the name *resupinata* is used in anticipation of the granting of the above application, and the specimen desinated by George & Ponsford (1938) and figured by Bond (1941) is regarded as the type of the species.

Little critical work has been done on the stratigraphical work on the accepted range of *S. resupinata* in Europe until these studies have been carried out.

The specimens from Babbinboon are all smaller than the type specimen of *S. resupinata* and the surface spines are much fewer in number. From studies of specimens from the Carboniferous of New South Wales neither of these characters appear to be of specific value.

The American *S. swallovi* Hall from the Burlington limestone of the Mississippi Valley, is related to the present material. It is of interest to note that both Paeckelmann (1930 and Demanet (1934) have included *S. swallovi* in the synonymy of



TEXT-FIG. 6—Scatter diagrams of *Schizophoria* cf. *S. resupinata* (Martin).
Upper. Length/length of muscle field.
Middle. Width/width of muscle field.
Lower. Length/width.

S. resupinata, and judging from the features of both species which have been described up till the present, this would seem to be correct. However important internal features of both species remain unknown and the safest course is to maintain the status of the American species until more information becomes available.

Family RHIPIDOMELLIDAE Schuchert, 1913
Genus RHIPIDOMELLA Oehlert, 1890

Rhipidomella SCHUCHERT & COOPER, 1932, Mem. Peabody Mus. Nat. Hist., vol. 1, pt. 1, p. 133.

DEMANET, 1934, Mem. Mus. Hist. Nat. Belg., vol. 61, p. 37–44, pl. 2.

Genotype: *Terebratula michelini* L'Eveillé 1835.

Remarks.—Schuchert & Cooper (1932, p. 133) have given an excellent account of the morphology of this genus, but there are a few points which need modification. In none of the Lower Carboniferous species from Australia is the "ventral valve markedly concave or showing a tendency in that direction," as is stated on p. 134. They are all distinctly convex or flattened anteriorly. The structure referred to as the "pedicle callist" is in my opinion the scar of a pedicle adjustor muscle. Dresser (1954, p. 22) is of a similar opinion.

In the genotype, and in fact in almost all species referred to this genus, the adductor field in the brachial valve is relatively small, and is partly or completely encircled by a low ridge rising from the brachiophore plates. Only the anterior scars are rounded and well defined, and in my opinion it may well be doubted that the subtriangular region between the adductor scars and the base of the cardinal process served as a basis for muscle attachment. In late Carboniferous and Permian times however, some species tend to increase the size of the adductor field and *two* distinct pairs of *rounded* scars are developed (Dunbar & Condra, 1932, p. 52; Stehli, 1954, p. 290). It may be of some significance that in both of the species in which this phenomenon is noted the valves are strongly convex, an uncommon feature in Lower Carboniferous species.

After an examination of populations of the genus from several localities and horizons in the Lower Carboniferous of New South Wales, several conclusions have been reached concerning the taxonomic value of certain morphological features. The outline of the valves is variable and the range of variation is similar in almost all populations. (Schuchert & Cooper [p. 134] believe that some Pennsylvanian and Permian species can be recognised on the basis of shape.) The form of the adductor scars in the pedicle valve is very variable within each species and does not appear to be a useful taxonomic character.

Populations have been distinguished on the basis of one or more of the following characters: inflation of the valves; the degree of impression and the proportions of the muscle field of the pedicle valve; the depth of impression of the muscle field of the brachial valve; the strength of the cardinal process; and finally the density of the costellae. All except the first and last of these are internal characters. It is interesting to note that both Weller and Demanet have been able to use the same characters in the subdivision of the genus in the Lower Carboniferous of North America and Western Europe respectively.

Range.—This genus ranges from the Silurian to the Permian. In Lower Carboniferous times it was world wide in its distribution.

RHIPIDOMELLA AUSTRALIS (McCoy)
Pl. 12, fig. 13–20

Orthis australis McCoy, 1847, Ann. Mag. Nat. Hist., vol. 20, p. 234, pl. 13, fig. 4,4a.
Rhipidomella australis McCoy. DUN, 1900, Rec. Geol. Survey New South Wales, vol. 7, part 2, p. 79, pl. 21, fig. 10,11.

Lectotype (here designated).—Internal mould of pedicle valve, labelled E 10663, Sedgwick Museum, Cambridge; from the Tournaisian of Lewinsbrook.

Description of topotypes.—Exterior: The shell is of average size for the genus, and is approximately as long as wide. Specimens are not strongly biconvex but this may be due to slight squashing during preservation.

The pedicle valve is rather flat, with its convexity increasing toward the umbo. The outline of the valve is variable from subpentagonal to elliptical and subcircular. The hinge line is short but its exact proportions are indeterminable due to the state of preservation. The cardinal area is very small. No median sinus is present and the commissure is rectimarginate. Nine to eleven costellae occur per 3 mm. at the anterior margin of the valve.

The brachial valve is more convex than the pedicle valve, the greatest convexity being in the posterior half. The outline of the valve tends toward circularity though some subpentagonal forms have been found. The umbo is small and obtuse. The valve is usually evenly convex but occasionally slight flattening may occur. A sinus is never present.

Interior: Internally the pedicle valve has short dental lamellae diverging at angles varying between 65° and 80° approximately. The muscle field is variable in size, its length and width averaging approximately half of the length and width of the valve respectively. A low ridge which is continuous with the anterior ends of the dental lamellae bounds the entire muscle field, and a low median septum divides it over the anterior two thirds of its length. The adductor scars are small and are situated in the median portion of the muscle field on very slightly elevated platforms which are poorly defined posteriorly. The diductor scars are semiflabellate and are marked by widely separated and sometimes indistinct radial ridges on their anterior portions. The pedicle adjustor muscle is not well defined.

The brachial valve has strong brachiophore plates, which so far as can be determined from the moulds, are pointed and free at their distal ends. They diverge at angles ranging from 70° to 88°. The cardinal process is variable in shape and size, in some cases the shaft being narrow and the myophore sharp, the whole structure being wedge-shaped, while in others the shaft is broader and the myophore rounded, the whole structure being slightly bulbous. Supporting the cardinal process is a strong rounded median ridge which extends to the edge of, or slightly beyond, the muscle field, becoming gradually lower in height anteriorly. The arrangement of the muscle scars is in no way unusual, the whole muscle field being bounded by an ill defined ridge.

Dimensions.—

(*See dimensions on page 53*)

Remarks.—(This species has not been found at Babbinboon. The description is included here to clarify the status of the species and to provide a basis for comparative work.)

McCoy's description was concerned mainly with the external outline of the valves, a feature which is very variable throughout populations of most species of the genus. He remarks that it may be distinguished from *R. michelini* (L'Eveillé) by "its wider hinge line, its much finer

Pedicle valves

Length	Width	Length of muscle scars	Width of muscle scars	Angle of divergence of dental lamellae
24 ±	23	12 ±	11	—
23	22½	14	13	67°
20	20	9	9	68°
19	20	10	9	75°
19	19	10	9	77°
19	19	9	8½	—
19	18½	9	9	—
18½	18	9	8½	—
18	18	11	11 ±	—
16½*	15	8	7	80° ±
14	13	8	7	72°

* Measurements from a photograph of the lectotype.

Brachial valves

Length	Width	Total length of muscle field	Total width of muscle field	Length of anterior adductor scars	Width of each of the anterior adductor scars
27	29	9	11	4½	4½
24 ±	24	7½	9½	4	3½
23	23 ±	7	8	4	3½
22	22	7	8½	3¼	3
21	21	7	10	4	4
21	20 ±	6½	7	3½	2½
20	20	6½	8	4¼	3

striae" and the "form of its muscular impressions." The length of the hinge line is very difficult to determine in the Lewinsbrook material and it is not a suitable character upon which to base comparisons. With regard to the other two characters, the Belgian specimens of *R. michelini* figured by Demanet (1934) have costellae of the same density as *R. australis*, and so far as I am able to determine there is no difference in the form of the muscle scars.

Dun (1900, p. 80) declares his belief in the distinctness of the two species *R. australis* and *R. michelini*, stating that the posterior scars in the brachial valve are not so clearly separated off, and the general area of muscle attachment is more elongate in the former than in the latter. Dun's comparisons were made with the *Rhipidomella michelini* of Davidson from the Carboniferous Limestone of England, not with the type material. He does not appear to have examined the range of variation found in populations of *R. australis*, even from the Clarencetown locality, since many of the specimens exhibit a distinctly quadruplicate muscle field in the brachial valve. In this character many specimens of *R. australis* are indistinguishable from the Belgian members of *R. michelini* as figured by Demanet (1934). Moreover, although the range of variation in the length of the muscle field of the brachial valve has never been described, the specimen figured by Demanet (1934, pl. 2, fig. 6a) falls well within the range of *R. australis*.

Without an examination of the type material, I am unable to distinguish between *R. australis* and *R. michelini*, but I prefer to retain *R. australis* until such an examination is possible.

The American *R. burlingtonensis* (Hall) from the Osagean is closely related to *R. australis* as also is *R. missouriensis* (Swallow) and *R. oweni* Hall & Clarke. Variation studies may well reduce the number of American species of this type.

Sarycheva & Sokolskaya (1952) have described and figured *R. michelini* from the Moscow Basin, but no detailed account or figure of the internal structures is given, rendering accurate comparison impossible. The range of this species in the area is given as Upper Tournaisian to Upper Carboniferous.

Range.—*R. australis* ranges through the

Lower Burindi Group of New South Wales, and a very similar form is found in marine incursions low in the Lower Kuttung Group.

RHIPIDOMELLA MYOSA, n. sp.
Pl. 12, figs. 6–12

Orthis (*Rhipidomella*) *australis* (McCoy). BENSON & DUN, 1920, Proc. Linn. Soc. New South Wales, Vol. 45, no. 179, p. 346, pl. 19, fig. 9.

Holotype.—F. 2651. University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: This species is rather small for the genus. The outline of the pedicle valve is variable from oval to subpentagonal, and it is convex with the greatest convexity toward the umbo. No flattening of the valve occurs toward the cardinal extremities. The venter is evenly rounded or very slightly flattened, but a sinus is never developed. The umbo is high and acute and the hinge line is slightly less than one third of the total width of the valve. The cardinal area is relatively high and slightly concave. The surface bears low rounded costellae which increase by bifurcation and intercalation and which number 9 or 10 per 5 mm. on the median anterior portion of the valve.

The brachial valve is slightly more convex than the pedicle valve, and it also has its greatest convexity in the posterior half. Its outline is variable from subcircular to subtriangular. A well defined medial flattening is present, its margins diverging from the umbo at an angle of 25° approximately.

Interior: The dental lamellae are short and are free over a distance of less than 1 mm. The teeth are strong. The angle of divergence of the dental lamellae ranges between 60° and 80° with an average of 75°. A small pedicle adjustor scar is developed in in the delthyrial cavity. The muscle field is deeply impressed posteriorly, the degree of impression increasing during ontogeny. Anteriorly the muscle field rises gradually to the general level of the shell. The diductor scars are broad and flabellate and their surface bears three to five radial ridges on their anterior half. The adductor scars are very variable in shape and in width. They are situated with their broadest part in the central portion of the field and are continued forward to the edge of the field on a high narrow ridge. As can be seen from the length/length of muscle field, and width/width of muscle field plots, there is a slight tendency to increase the relative area of muscle attachment during ontogeny.

In the brachial valve there is a high rounded median ridge which reaches to the middle of the valve. From its posterior end the cardinal process arises very abruptly. This is a large structure with a long rounded shaft and an unexpanded myophore. The brachiophore plates abut the base of the cardinal process and so far as I can determine are long and pointed. They bound the posterior tips of the muscle field. The muscle scars are deeply depressed and clearly differentiated.

Dimensions.—

(*See dimensions on page 55*)

Remarks.—Benson & Dun described this form as *Orthis* (*Rhipidomella*) *australis* (McCoy). They record the dimensions of one specimen only: "Breadth, 21 mm. length, 19 mm. and depth or thickness, 5 mm." I have found no specimens as large as this.

R. myosa, n. sp., differs from *R. australis* (McCoy) in the following features: (1) In general it is distinctly smaller in size. However, size being a notoriously deceptive taxonomic feature, little weight is placed upon this.

(2) The ornament is consistently and distinctly coarser. An examination of members of this genus from many Carboniferous localities in New South Wales have showed great constancy in this character in spite of great variation in the nature of the associated sediments, *R. myosa* being the only significantly variant species yet discovered. The world over, the dominant Lower Carboniferous species of *Rhipidomella* have a constant density of the costellae as can be observed for example from the work of Demanet (1934) on *R. michelini* (L'Eveille) and its variants, and that of Weller (1914).

(3) The cardinal process is larger and arises more abruptly from the median ridge.

(4) The ratios L.M.F./L and W.M.F./W increase at a greater rate during ontogeny. Unfortunately small topotypes of *R. aus-*

Pedicle valves

Length	Width	Length of muscle field	Width of muscle field	Angle of divergence of dental lamellae
14	14	9	8½	80°
14	14½	9½	10	70°
12	13½	8	8	75°
14½	15	8½	8	80°
16	15	10	9½	60°
11½	12	5½	5	—
9	9	4½	4½	—
13	11½	7	6½	80°
10	10	5½	6	75°
10½	11½	6½	6½	75°
8½	8½	4	5	80°
12	11	6½	7	—
7½	8	3½	3	80°
12	11½	7	6½	—
8	8	5	4½	—
15	15½	8½	8½	—
12	12	8½	7	65°
15	16	10	10	70°
14	14½	9	10	—
7	7½	4	3½	—
9	10	5	5	—
9½	11	5	6	—
11	12	7	8	—
13½	12	8	7½	—
13	14	8	8	—
8	8½	5½	5	—
10	10	5½	5½	80°

Brachial valves

Length	Width	Total length of muscle field	Length of anterior adductor scars	Total width of muscle field	Width of each of the anterior adductor scars
14	14	5	3	6	2½
16	16	5	3½	6½	3¼
13	14	4½	2¾	6	2½
11½	11½	5	3½	6	2½
11½	13	4	—	6	2½
12½	12½	—	3½	6	2½
9½	11	3½	—	4½	—
12	12½	5	3	4½	2
9½	9	3½	—	4	1½
9½	11	4½	—	6	—
13	12	4½	3	6	2¼
14½	14	—	—	6	2
13	13	5	3	6	2½
14½	13½	4½	—	6	—
13½	—	5	3	6¼	2¾

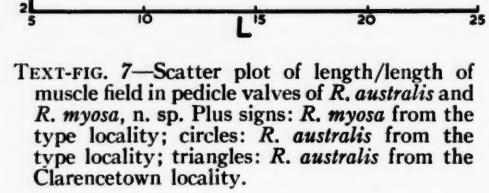
tralis are very rare, and to cover the ontogeny of this species it has been necessary to refer to a population from the Clarencetown—Glen William area. The adults of this population are, in all respects closely comparable with those from the type locality and there is no doubt that they are conspecific. These localities are approximately 15 miles apart, are within the same geological structure and on similar stratigraphic levels.

(5) The adductor scars in the brachial valve are more deeply impressed and the median ridge is narrower and higher.

(6) Finally, both valves are relatively more convex.

Two American species are comparable with *R. myosa*, n sp. *R. theimi* White from

TEXT-FIG. 7—Scatter plot of length/length of muscle field in pedicle valves of *R. australis* and *R. myosa*, n. sp. Plus signs: *R. myosa* from the type locality; circles: *R. australis* from the type locality; triangles: *R. australis* from the Clarencetown locality.



TEXT-FIG. 8—Scatter plot of width/width of muscle field in pedicle valves of *R. australis* and *R. myosa*, n. sp. Same symbols as Text-fig. 7.

the Upper Kinderhook limestone is very similar in size, shape, and internal structure but has finer ornament and a pronounced sinus on the anterior of the pedicle valve. Weller (1914, pl. 20, fig. 30–35) has figured a specimen which he states is similar to the type of *R. diminutiva* Rowley. This specimen differs from the adults placed in the same species by Weller in its much coarser ornament. In form and in ornament it is very similar to *R. myosa*.

Range.—This species so far known only from the type locality, Upper Tournaisian.

Superfamily PRODUCTACEA Maillieux, 1941
Family DICTYOCLOSTIDAE Stehli, 1954
Genus DICTYOCLOSTUS Muir-Wood, 1929

Dictyoclostus MUIR-WOOD, 1929, Ann. Mag. Nat. Hist., vol. 5, p. 103 [in part]. SUTTON, 1938, Jour. Paleontology, vol. 12, p. 562–564 [in part], pl. 64, fig. 1–8.

Spinifrons STEHLI, 1954, p. 318–19, pl. 20, fig. 6–10.

Genotype: *Productus semireticulatus* (Martin)

Diagnosis.—This genus includes quadrate to semicircular productids on which the ornament of the pedicle valve consists of radial costae at all growth stages, concentric ribs on the visceral disc and large spines which are irregularly arranged on the flanks, trail and lateral portion of the ears. Smaller insignificant spines may occur on the visceral disc. There may or may not be one or two rows of spines along the cardinal margin. The brachial valve is aspinose but otherwise is ornamented similarly. Internally the pedicle valve is usually thickened along the hinge and may be ginglymoid. The brachial valve has well developed cardinal ridges which are usually deflected around the lateral margins of the valve, and may even be very faintly continued around the anterior margin. Teeth and cardinal areas are not developed.

Remarks.—Of the British species originally included in this genus by Muir-Wood, I include such species as *D. pinguis* (Muir-Wood), *D. teres* (Muir-Wood), *D. multispiniferus* (Muir-Wood) and *D. vaughani* (Muir-Wood), together with the American species *D. fernglenensis* (Weller), *D. burlingtonsis* (Hall) and *D. crawfordsvillensis* (Weller), The genus *Spinifrons* Stehli from the Permian of Texas is regarded as synonymous with *Dictyoclostus*, from the genotype of which it differs only in the presence of a group of enlarged spines on the anterior part of the trail. As is pointed out by Stehli, *D. pinguis* Muir-Wood (which is found associated with, and is in other respects closely similar to, *D. semireticulatus*) has a spine arrangement similar to *Spinifrons*. The proliferation of genera upon the basis of such minor variations in spine arrangement, especially when it can be shown that spines on the trail are frequently intraspecifically variable, is, in my opinion indefensible.

Ivanov (1935) in an emendation of *Dictyoclostus* Muir-Wood states that "the area is hidden, narrow and groove-like with a wide delthyrial notch; the area may

occasionally be vestigial or even lacking." (English summary). Sutton (1938, p. 562) also states that "occasionally a linear cardinal area occurs," and Dunbar & Condra (1932, p. 213) indicate that a linear cardinal area may be developed as an individual variation. Most species of *Dictyoclostus* have a thickened hinge on the pedicle valve, and if during preservation the brachial valve slips forward slightly, a linear strip of this thickened region, which superficially resembles a cardinal area, is exposed. I have never observed mixoperipheral growth in a dictyoclostid and therefore prefer to maintain Muir-Wood's original opinion that a cardinal area is not developed.

Both of the new species here ascribed to *Dictyoclostus* have adductor scars in the brachial valve which are in the process of differentiation into two pairs, the degree of differentiation being variable within each species. So far as I can determine, British representatives of *D. semireticulatus* have simple brachial adductor scars, though it ought to be added that this feature has been described only in a few specimens. Sarycheva (1949, p. 88) in a description of the characters of *Dictyoclostus* based upon specimens from the Lower Carboniferous of the Moscow Basin, states that the muscle impressions of the brachial valve are "branched, second pair not clear." Her figure on pl. 4, fig. 2 of *D. pinguis* var. *munda* shows a partial division of the scars quite similar to that seen in some specimens of *D. simplex*, n. sp. Muir-Wood (1931, p. 151) has described specimens of *D. teres* from the C_1 and C_2 sub-zones of the Tuedian Beds in Northern Cumberland and Roxburgshire, in which the adductor scars in the brachial valves are

> distinctly divided into posterior and anterior scars. The anterior is set on a slight ridge and is less dendritic than the posterior adductor. The brachial impressions are given off half way down the length of the adductors.

This description would cover both of the new species described herein. It is worthy of note also that the specimen of *D. inflatus* figured by Cooper (1944, pl. 136, fig. 13) appears to have partial subdivision of the muscle field. The presence of these subdivided adductor scars does not seem to be correlated with any other feature and this together with its wide distribution suggests that it may be recurring feature within *Dictyoclostus*.

Noteworthy also is the marginal ridge in *D. paradoxus*, n. sp. At one end of the range of variation are specimens in which the marginal ridge is present along the hinge and one or two millimeters anterior to it, and at the other end are the occasional specimens in which a very faint ridge completely encircles the visceral disc.

Range.—Carboniferous to Permian. It is world wide in its distribution.

DICTYOCLOSTUS SIMPLEX, n. sp.
Pl. 13, fig. 1–8; Text-fig. 9

Productus semireticulatus (Martin) BENSON & DUN, 1920, p. 344, pl. 19, fig. 2–5, non fig. 6 and 7.

Holotype.—F. 2072 University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

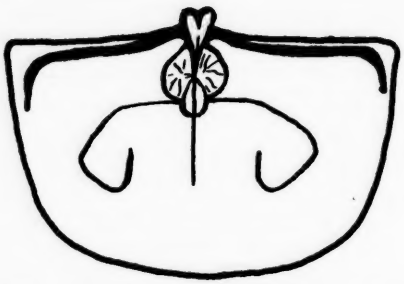
Description.—Exterior: The shell is of average size for the genus. The visceral disc is much wider than long, the greatest width being at the hinge. The cardinal extremities are most frequently mucronate. The pedicle valve is strongly gibbous being most strongy convex in the umbonal region. The umbonal portion bears no sinus, but the median portion of the valve is usually flattened and the trail may be either flattened or bear a broad shallow median sinus. The auriculations are only slightly flattened and are not sharply divided from the body of the valve. The umbo is small and pointed. There are twelve to sixteen costae per 10 mm. on the anterior part of the trail. The costae increase both by intercalation and bifurcation. Concentric ribs are continuous over the visceral disc, up to sixteen of them being developed in adults. There are no spines on the cardinal margins. Spines of two sizes are developed. The larger ones which may be up to 1½ inches in length and 2 mm. maximum diameter are gently tapering and have a large internal cavity. These leave large pits with raised rims on the internal surface of the shell. One or two such spines occur on the trail just anterior to each cardinal extremity, and in most specimens three of them occur irregularly arranged on the anterior part of the trail, although in others this number is increased to four or even five. The costae anterior to these large spines are much broader than normal. Very

small spines are rarely and irregularly derived from the costae. These have no distinct mark on the interior of the shell.

The brachial valve is concave to geniculate, and the visceral disc is gently concave. The auriculations are depressed. The umbo is small and concave. A faint fold is occasionally developed on the edge of the visceral disc and on the trail. There are up to sixteen concentric ribs developed on the visceral disc, and the costae are of the same type and number as those of the pedicle valve. The valve is aspinose.

Interior: The pedicle valve is slightly thickened in the umbo and along the hinge. A shallow ginglymus is developed. The shell thickening is in some specimens continued anteriorly for a short distance from the cardinal extremities around the visceral disc. The adductor platforms are low but distinct and are long and narrow. In most cases the width of the whole adductor field is between 2.5 and 3 mm., and its length two thirds of the length of the visceral disc. The adductor platforms are separated by a shallow depression. The diductor scars are slightly impressed into the shell and are large and flabellate. Their surface is longitudinally striated.

Marginal ridges are well developed along the hinge line of the brachial valve. The cardinal process is small and has a bilobed ventral tip and trilobed dorsal surface. The adductor muscle scars are differentiated into a broad dendritic postero-lateral pair on slightly raised platforms, and an antero-median pair which are elongate-oval in outline and are usually slightly higher. The postero-lateral pair enclose the posterior half of the other pair. There is considerable variation in the degree of distinction of these two pairs of scars. The brachial ridges are not visible on most specimens but in those specimens in which they are developed they arise from the junction between the two sets of muscle scars, run laterally almost parallel with the hinge and then swing around in open loops (Text-fig. 9). The median spetum is a complex structure and is very variable. It arises at the base of the cardinal process where it is very broad, and tapers rapidly to a point between the two antero-median



TEXT-FIG. 9—Sketch showing the internal structure of a brachial valve of *D. simplex*, n. sp., ×1.5.

adductor scars. This posterior portion of the septum is either evenly rounded, or more frequently bears a median groove of varying length. In some specimens this posterior portion is continuous with a narrow anterior septum but in others there is a distinct break between the two. The anterior portion may gradually increase its height and be sharply truncated at its tip or it may remain a low sharp ridge. It reaches a point two thirds of the length of the valve from the umbo. In those specimens in which brachial ridges are developed the surface of the visceral disc posterior to these ridges is densely pitted and that anterior to them is costate. In other specimens the whole surface is costate.

Dimensions (mm.).—

Pedicle valves

Length	Length on curvature	Width at hinge	Height	Length of adductor field
—	59	31	—	—
26	56	35	17	—
—	56	32	—	—
—	55	27	—	—
—	54	27	—	—
—	53	34	—	—
25	53	33	19	—
—	52	28	—	—
—	52	28	—	—
—	51	36	18	—
24	51	35	16	—
—	50	37	—	—
—	50	30	—	—
—	50	30	—	—
—	49	30	—	—
—	49	27	—	—
—	49	27	—	15
21	49	33	17	—

(*Continued on next page*)

Pedicle valves

Length	Length on curvature	Width at hinge	Height	Length of adductor field
20	48	26	17	—
—	48	30	—	16
—	47	28	—	—
—	46	30	—	17
—	46	29	—	16
—	46	32	—	—
—	46	28	—	—
—	46	28	—	14
—	46	27	—	—
—	46	27	—	—
—	45	26	—	14
21	45	27	15	13
—	45	31	—	14
19	45	24	14	14
—	44	30	—	14
23	44	26	14	15
—	44	30	—	14
—	42	31	—	—
—	41	28	—	—
—	41	25	—	14
—	41	29	—	15
22	40	32	13	15
—	40	30	—	—
21	40	33	13	—
—	40	35	—	—
19	39	24	12	13
20	38	27	15	—
—	38	31	—	13
22	36	30	14	14
20	32	27	—	—

Remarks.—No British species is closely comparable with *D. simplex*, the closest being *D. vaughani* (Muir-Wood) which differs in the nature of the ribs on the pedicle valve, the arrangement of the spines, the more elongate trail and the steeper lateral slopes.

In size, form, ornament and the arrangement of the spines *D. simplex* is similar to the German specimens from the Upper Viséan referred by Paeckelmann (1930) to *Productus* (*Dictyoclostus*) spp. 2 and 3 aff. *pugilis* Phillips.

D. burlingtonensis (Hall) as figured by Weller (1914) appears to be most closely comparable of all overseas species. There appear to be slight differences in the strength of the median sinus in the pedicle valve and the length of the brachial median septum. I have been unable to find a description of the adductor muscle field of the brachial valve of *D. burlingtonensis* and it is yet possible that this may prove an additional point of distinction. This species is typical of the Burlington limestone of Iowa, an Upper Tournaisian formation.

Nalivkin (1937) has recorded the occurrence of similar forms which he refers to *D.*

Brachial valves

Length	Width	Length of median septum	Width of anterior adductor scars	Length of anterior adductor scars	Total length of adductor scars	Total width of adductor scars	Distance between outer limits of brachial ridges
21	35	14	3½	5	8	9	22
21	34	15	—	4	8	—	24
22	34	14½	4½	5	8	7½	—
—	34	13	4½	4½	7½	9½	22
—	33	15	—	—	7½	10½	22
—	33	14	5	5	10	10	—
—	32	16	4½	5½	8½	9	22½
—	32	12	4	6¼	9	8	19
20	30	13	3¼	4	8	8½	—
—	30	13½	4	4	7	—	—
19	30	12	—	—	7½	7	—
—	—	14	3½	5	7½	7½	20
20	—	13	4½	—	10	—	21½
18	28	13	4½	5	7	9½	23
16	27	11	4½	5	7	9	21

Note: Because of the difficulty of determining the posterior limits of the adductor scars in the pedicle valve, the length of the adductor scar given in the tables of measurements for this genus is the distance from the tip of the umbo to the anterior edge of the scars *measured around the curvature*. The length of the median septum is measured from the base of the cardinal process.

burlingtonensis Hall from the Russakov and Ishim beds of Upper Tournaisian and Lower Viséan age respectively, in north-eastern Kazakhstan.

Range.—Upper Tournaisian; found at many localities in the upper part of the Lower Burindi Group of New South Wales.

DICTYOCLOSTUS PARADOXUS, n. sp
Pl. 13, fig. 9–17

Productus semireticulatus (Martin) BENSON & DUN 1920, p. 344 [in part]: text-fig. 11.

Holotype.—F. 1972 University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The shell is small, with a hinge line slightly less in width than the maximum width of the shell.

The visceral disc of the pedicle valve is subsemicircular in outline. The lateral profile is semicircular to subgeniculate. The umbo is relatively large and pointed, and slightly overhangs the hinge line. The cardinal extremities are mucronate in most specimens. The venter is evenly rounded or slightly flattened. The costae are well developed, increasing both by intercalation and bifurcation, and numbering sixteen to twenty (average eighteen) per 10 mm. on the median anterior portion of the trail. Concentric ribs occur on the visceral disc only, the number present ranging from thirteen to seventeen. Most specimens have a spine on the lateral part of the trail just anterior to each auriculation, and three or four spines are scattered irregularly on the trail.

The brachial valve is geniculate to sharply rounded. The visceral disc is gently rounded and the auriculations are flattened. The ornament is similar to that of the pedicle valve, except that it is aspinose.

Interior: The pedicle valve is thickened in the umbo and along the hinge line forming a slightly ginglymoid articulation. Strong ridges arise from the hinge line on either side of the umbo and run around the inner margins of the auriculations on to the lateral parts of the trail where they fade out. Some specimens show a faint continuation of this ridge around the whole valve. The auriculations appear to be very flattened in internal moulds as a result of this thickening.

The brachial valve has cardinal ridges of variable strength which are set at angles up to 15° to the hinge line across the posterior portion of the valve. They swing across the inner edge of the auriculations and thence down the lateral margins of the visceral disc where they become obscure. In occasional specimens a faint marginal ridge completes the circuit of the anterior margin of the visceral disc. The cardinal process is short and squat and is bilobed ventrally and trilobed dorsally. It is supported on a broad low median ridge which is variable in width and height, and which never extends more than three-quarters of the length of the muscle scars. Anterior to this is a blade-like septum which also is very variable in its strength. In the best developed specimens it gradually increases in height to a point two-thirds of the distance from the umbo to the edge of the visceral disc where it is sharply truncated. A small knob-like inflation may be present at its anterior tip. The adductor scars are rather poorly defined, and there is considerable variation in their arrangement. In some specimens there is a clear differentiation into an elongate antero-central pair and a broader but shorter postero-lateral pair of scars, but in others the differentiation is incomplete. Dendritic markings have not been definitely observed but longitudinal markings are present on some specimens. The brachial ridges are variable in strength and conformation, in some specimens being indistinguishable, in others subsemicircular platforms and in yet others, low crescentic ridges.

Dimensions (mm.).—

(*See dimensions on page 61*)

Remarks.—One of the most significant features of this species is its variability, in the development of the marginal ridge and the differentiation of the adductor scars in the brachial valve, and in the disposition of the anterior spines. The significance of this variation is discussed under the remarks on the genus.

Benson & Dun (1920) have referred this species to *Productus semireticulatus* Martin, their determination being based upon a

Pedicle valves

Length	Length of curvature	Width at hinge	Height	Length of adductor scars	Width of adductor scars
20	35	16	—	—	—
20	33	17	10	—	—
18	32	16	10	—	—
—	32	15	11	12	2
—	32	—	11	13	2
17	31	—	11	12	2½
17	31	16	11	—	—
16	31	16	11	—	—
18	30	17	—	10	1½
18	30	16	10½	11	1½
16	29	15	9	9	2¼
17	28	—	9½	11	2
16	28	17	7	—	—
17	28	15	9	—	—
17	28	15	9	11	1½
16	27	16	—	12	2
16	26	15	8	—	—
17	26	20	8	—	—
—	25	15	—	10	1¾

Brachial valves

Length	Width at hinge	Length of adductor scars	Width of adductor scars	Length of median septum	Distance between outer limits of brachial ridges
15	23	—	—	—	—
15	21	5	6½	10	15
14	20	5	3½	8½	—
—	19	4½	4½	8	13½
—	18	5	6½	8	—
13	17½	4½	—	8	12½
16±	17	—	—	9½	13
12	17	5	6	8½	14
16	16	6	4½	9	13½
—	16	5½	5±	9½	—
—	16	5	—	8½	12
12	16	—	—	—	—
13	16	—	—	—	—
11	15	5	5	8	12
13	15	—	—	—	—

Note: Width of the hinge has had to be estimated in almost every case because the cardinal extremities are damaged.

study of the external form and the ornament only. In fact there is little relation between the typical *Productus semireticulatus* as described and figured by Muir-Wood (1928) and *D. paradoxus*, n. sp. Of the British species the most closely allied is *D. teres* Muir-Wood from the C zone, but it differs in the greater number of spines along the trail. Although the internal structure of *D. teres* was not originally described by Muir-Wood, she (1931, p. 151) has described it in specimens from Cumberland which she refers to that species. The adductor scars in the brachial valve are distinctly differentiated into anterior and posterior pairs, and the "lateral ridges diverge slightly from the hinge-margin and are sharply recurved anteriorly from near the cardinal extremities." This is very similar to the structure of *D. paradoxus*.

The German *D. bergicus* Paeckelmann from the Viséan of Ratingen is remarkably similar to *D. paradoxus*. It is worthy of note that the pedicle valve of this species is also thickened along the hinge line and around the lateral margins of the visceral disc, though no mention is made of a marginal rim in the brachial valve.

D. mesialis (Hall) from the Keokuk limestone in North America resembles *D. paradoxus* in size and the subgeniculate curvature of the pedicle valve, but differs in its coarser costation, greater variability in the development of the sinus and in the presence of spines along the cardinal margin. Unfortunately no description of the internal structure of this species is available.

DICTYOCLOSTUS sp.
Pl. 13, fig. 18,19

Description.—In the collections are four brachial valves which obviously belong to one species and one pedicle valve which may also belong to it.

Exterior: The brachial valves are wider than long but since all the specimens are broken no accurate measurements are possible. Juvenile specimens are gently and adults more strongly concave. No trail appears to have been developed although it is not possible to be certain of this. A pronounced fold originates on either side of the umbo and proceeds to the posterolateral margins, their crests making an angle of 15° with the hinge. These folds become progressively broader away from the umbo. A very low median fold is present on the anterior of the valve. The surface of the valve bears rather coarse costae (five or six per 5 mm. at the anterior edge of the valve) which increase by intercalation, and which are crossed by strong concentric ribs. At the junction of the ribs and costae pronounced nodes are developed, but they do not bear spines. On the largest specimen there are approximately twenty ribs.

Interior: The valves are slightly thickened along the hingeline. The cardinal process is distinctly bifid ventrally. From its base arise two strong ridges which bound the folds mentioned earlier. These ridges are not the result of shell thickening but of plication. The median septum is long, straight and tapering, and divides an undifferentiated pair of dendritic adductor scars.

Dimensions (mm).—

Length	Length of median septum	Length of muscle field	Width of muscle field
25 ±	16	6½	7

Remarks.—The folds diverging from the umbo give this species a particularly characteristic appearance. They have not been described in any other species of which I am aware.

Family ECHINOCONCHIDAE Stehli, 1954
Genus ECHINOCONCHUS Weller, 1914
ECHINOCONCHUS GRADATUS Campbell

Echinoconchus gradatus CAMPBELL, 1956, Jour. Paleont., vol. 30, p. 474, pl. 49, fig. 14–18.

Remarks.—Since the first publication of the description of this species more topotype material has come to light showing the spine arrangement on the pedicle valve. The major spines bases are very elongate, low posteriorly and rise to a maximum height anteriorly where they are sharply truncated. They stop short of the anterior edge of the lamellae. Between their front edges and along the edge of the lamellae two or three irregular rows of very fine spine bases occur.

Genus WAAGENOCONCHA Chao, 1927
WAAGENOCONCHA DELICATULA Campbell

Waagenoconcha delicatula Campbell, 1956, Jour. Paleont., vol. 30, p. 471, pl. 50, fig. 1–9.

Remarks.—I have nothing to add to the original description of this species.

Superfamily CHONETACEA Shrock & Twenhofel, 1953
Family CHONETIDAE Hall & Clarke, 1895
Genus CHONETES Fischer
Genotype: *Terebratulites sarcinulatus* Schlotheim, 1820

Remarks.—Ramsbottom (1952, p. 11) has clearly shown that the genotype of *Chonetes* is *Terebratulites sarcinulatus* Schlotheim, a Lower and Middle Devonian form from the grauwacke of Rammelsberg in the Harz. This species is difficult to interpret since the description and illustrations of Schlotheim are inadequate (only pedicle valves are figured), and according to Kayser (1889, p. 63) the type specimens are not housed with the Schlotheim collection in the Berlin Museum of Natural History.

Many subsequent European authors have referred European material from the Lower and Middle Devonian to this species (see the synonymy given by Maillieux 1932, p. 33–36). A study of the descriptions and illustrations given by the authors there

listed indicates that *C. sarcinulatus* is a chonetid of medium size, semicircular to subrectangular in outline, and with a long hinge approximately equal to the greatest width of the shell. The surface is ornamented with approximately fifty striae which may dichotomise or remain simple. Internally the pedicle valve has a low median septum which extends beyond the middle of the valve, and the brachial valve has a very weak median septum and two slightly oblique septa which are higher and longer, extending to within 1 to 2 mm. of the anterior margin of the valve.

If this should prove to be an accurate description of the species then a new genus will need to be erected for the multistriate species in which the brachial valve has a long median septum flanked by two very short septa which divide the adductor scars. To this group belong forms similar to that herein referred to *Chonetes careyi* n. sp., the European *C. dalmaniana* and *C. laguessiana*, the Russian *C. carboniferus* and *C. dalmanoides* and the American *C. illinoisensis* and *C. multicosta*.

However, until topotype material of *C. sarcinculatus* has been restudied and the above observations confirmed, I continue to maintain the broad genus *Chonetes* auct.

CHONETES CAREYI, n. sp.
Pl. 12, fig. 21–26

Holotype.—F. 2666 University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The pedicle valve is moderately strongly convex. The greatest width is at the hinge-line or just anterior to it, and the cardinal extremities are angular. In general the outline of the valve is semicircular though there is a strong tendency to rectangularity in some specimens. There is no sharp change in slope between the ears and the body of the valve. The venter is either flattened or bears a shallow sinus. The spines along the cardinal margin are difficult to prepare for observations, but two specimens have been found showing at least four large spines on either side of the umbo and another showing six or seven. It has not been possible to determine the relative sizes of the spines. The cardinal area is rather high and markedly triangular. The delthyrium is broad and its apex is covered by a very small highly convex calluslike pseudodeltidium. The surface is ornamented with very fine striae, adult specimens bearing between 110 and 150. On the ears the striae become very indistinct. On the central portion of the valve at 5 mm. from the umbo there are 10–15 striae per 3 mm.

The brachial valve is variable but usually only slightly concave. The ears are flattened. The dorsum may be either flattened or bears a very shallow fold. The umbo is flattened. A very narrow cardinal area is developed.

Interior: The teeth are large. A narrow sharp median septum extends from the umbo one quarter to one third of the distance to the anterior margin. The adductor scars are very poorly defined. They are situated close to the median septum and are elongate in outline being pointed posteriorly and rounded anteriorly. The diductor scars are distinctly impressed posteriorly but their limits are indistinguishable anteriorly, and they are not clearly divided from the adductor scars. The lateral and anterior portions of the surface are strongly papillose.

From the base of the squat cardinal process two short thick socket plates extend laterally almost parallel with the hinge line. The low median septum may arise from the base of the cardinal process or just anterior to it, and extends one half the length of the valve. Two short (2 mm.) ridges arise in the depressions between the socket plates and the median septum. Presumably these separate the two pairs of adductor scars. However the inner pair of scars has not been observed. The outer pair is subtriangular but its anterior margins cannot be clearly defined. The whole surface except that of the ears is papillose.

Dimensions (mm.).—

(*See dimensions on page 64*)

Remarks.—In Australia, species of this type have been variously referred to *Chonetes laguessiana, C. hardrensis* and *C. papillionacea*, from all of which there are marked differences.

Of the English species it is perhaps closest to the forms referred by Davidson to *C. dalmaniana* de Koninck, and of the German forms, *C. hemisphaericus* von

Pedicle valves

Length	Width	Width at hinge	Height	Width of adductor scars	Total width of muscle scars	Total length of muscle scars
15	22	21	4½	—	—	—
13½	19	15	3½	—	—	—
12	18	—	—	1½	8	7
12	16½	14	—	—	—	—
11½	17	16	—	—	—	—
11	16	15½	4	—	—	—
11	16	15	2½	—	—	—
11	16	—	4½	1½	6	4½
10	15	14	2½	1½	—	—
9	13½	—	3½	1½	5	3½

Brachial valves

Length	Width	Width at hinge	Length of median septum
12½	18	16½	—
12	20±	—	6
11½	18	—	5
11	17	17	5
10½	17	—	5
9½	15	—	4
9	17½	16	—
8½	16	—	3½
8½	13½	—	3½
7	13	12½	—
6½	12	12	—
6	11	11	—

Semenew emend. Paeckelmann from the Kulm, bears it most resemblance.

In America there are several species similar to *C. careyi*, n. sp., which range from the Kinderhook to the Chester Group. They exhibit considerable variation in the density of the development of the striae but this seems to have no stratigraphic significance. The descriptions of the internals of the pedicle valves are almost invariably unsatisfactory, but the brachial internals of *C. illinoisensis* Worthen and *C. missouriensis* Weller from the Osage and Kinderhook groups respectively are essentially similar to *C. careyi*.

Sokolskaya (1950) has referred specimens

EXPLANATION OF PLATE 13

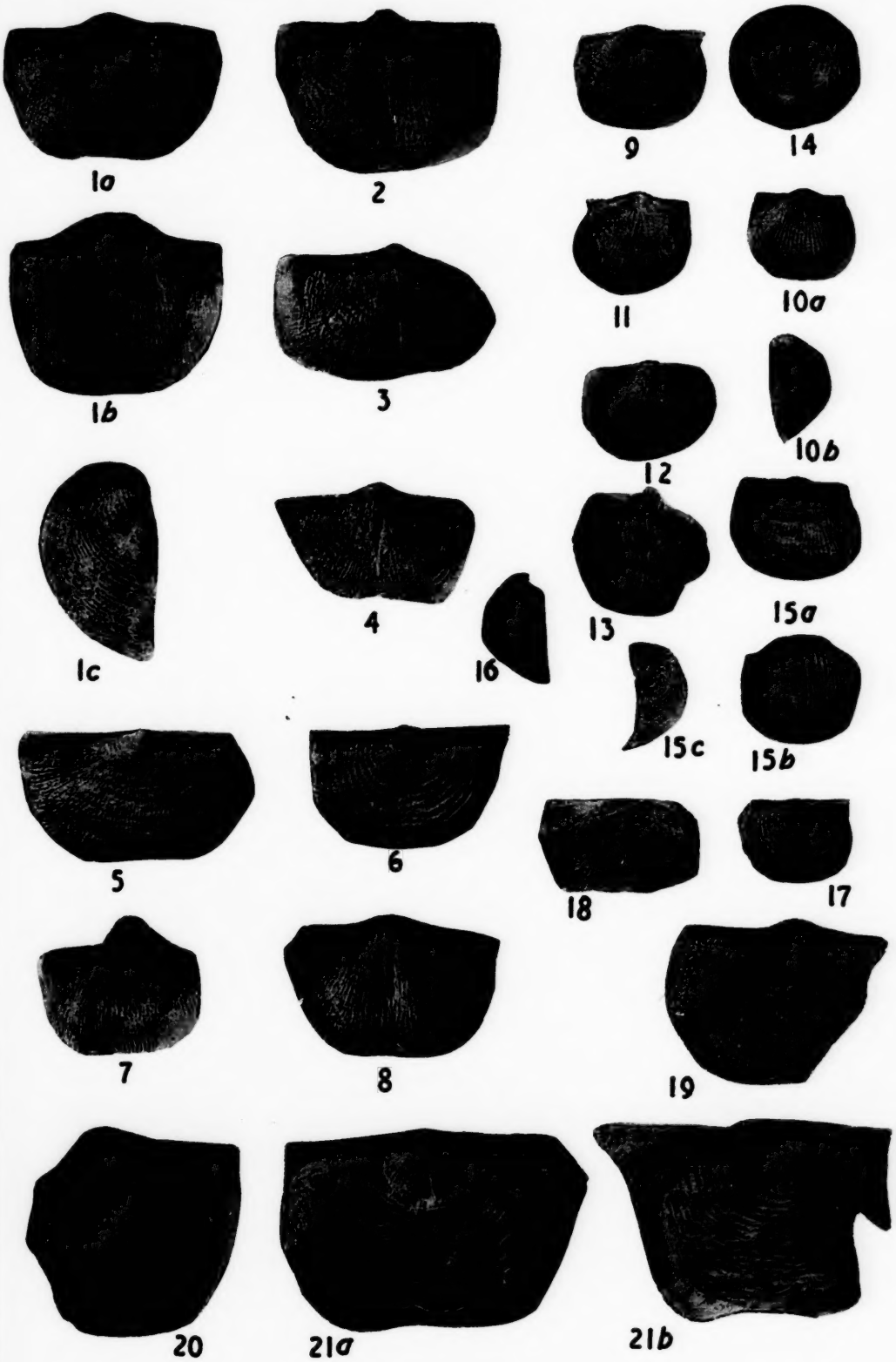
(All specimens natural size and from Watts, Babbinboon unless otherwise stated.)

FIG. *1–8—Dictyoclostus simplex*, n. sp., *1a-c*, ventral anterior and lateral views of a pedicle valve, holotype, F. 2072; *2–4*, interior views of three brachial valves F. 2106, F. 2885 and F. 2117; *5,6*, visceral discs of two pedicle valves, F. 2113 and F. 2052; *7,8*, internal molds of two pedicle valves, F. 2015 and F. 2065. (p. 57)

9–17—Dictyoclostus paradoxus, n. sp., *9*, internal mold of a pedicle valve; note the auriculations; F. 1979; *10a,b*, ventral and lateral views of the internal mold of a pedicle valve, F. 1966; *11–13*, casts of three brachial interiors; note the faint marginal ridge in fig. 13, which specimen is ×1.3, F. 1963, F. 2886 and F. 1947; *14*, anterior view of the mold of a pedicle interior showing the large pits left by the spines, F. 1951; *15a-c*, ventral, anterior and lateral views of a complete specimen; note the large spine base together with the enlarged costa anterior from the ear in fig. 15c; holotype; F. 1972; *16*, lateral view of the mold of a pedicle interior showing the thickened ridge running along the lateral margins from the cardinal ridge; note also the impression of the large spine base anterior to the ear; F. 1979; *17*, external mold of a brachial valve, F. 1977. (p. 60)

18–19—Dictyoclostus sp. Two molds of brachial interiors, F. 2609 and F. 2610. (p. 62)

20–21—Leptaenella cf. *L. analoga* (Phillips). *20*, mold of brachial interior, F. 2538A; *21a,b*, internal and external molds of pedicle valve, F. 2537A,B. (p. 41)


1a
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14
11
10a
1b
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10b
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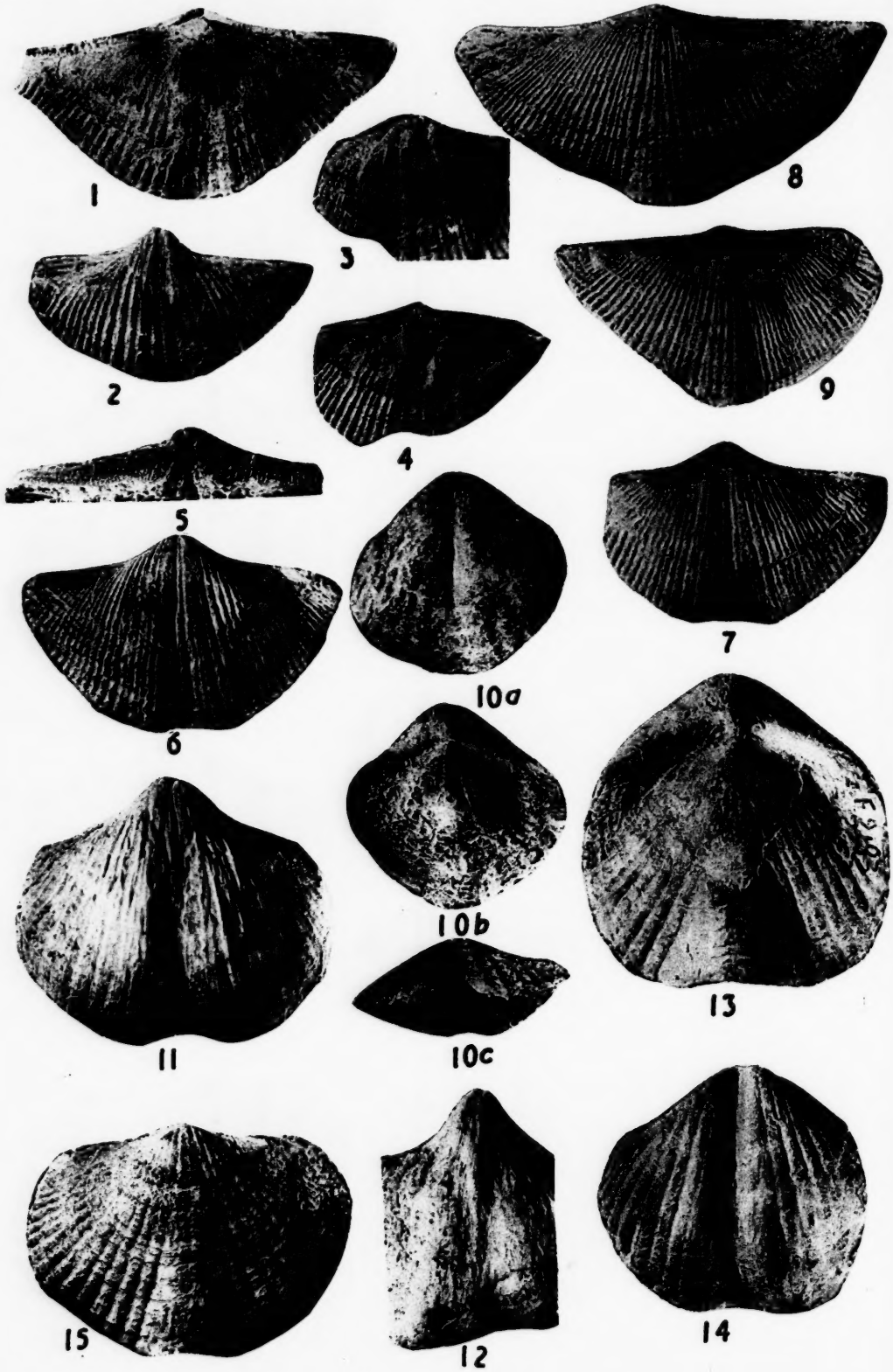
21a
21b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from the Tournaisian beds of the Russian platform to *Chonetes dalmanianus* de Koninck. These are comparable with *C. careyi* in all features except the slightly coarser striae.

Range.—Upper Tournaisian. At present it is known only from Babbinboon.

Genus RUGOSOCHONETES Sokolskaya, 1950
Genotype: *Orthis hardrensis* Phillips.

Description.—See Sokolskaya (1950, p. 23).

Remarks.—The generic position of the specimens described herein is in doubt.

As Maxwell (1954, p. 20) has pointed out, Sokolskaya, in citing "*Orthis hardrensis* Phillips 1841, p. 138, pl. 58, fig. 104 b–d," as the genotype of *Rugosochonetes*, has automatically selected that specimen, which comes from the Viséan of Hardraw in Yorkshire, as the lectotype of *O. hardensis*. (Phillips' material included specimens from the Lower Devonian of Devon as well as the Carboniferous of Yorkshire.) So far as I am aware this is the first definite designation of the lectotype, though suggestions that the Carboniferous specimens should be considered as the types have been made previously by several authors (e.g., McCoy, 1855, p. 454–455; Smith, 1925, p. 86 footnote 1, fide Ramsbottom in litt.).

According to Smith (op. cit.) it is very doubtful whether the original types are now in existence.

Sokolskaya in her description of the genus has depended on Russian specimens which have been assigned to *Chonetes hardrensis*, and apparently has not examined topotype material. So far as I am aware neither Phillips' specimens nor topotype material has been redescribed, and since Phillips' original description is only vaguely general concerning the internal structure of the species, it is impossible to be certain that the Russian material has been correctly assigned.

By courtesy of Drs. J. Selwyn Turner and Derek Moore of Leeds University I have obtained a collection of chonetids from the Hardraw Scar area. Though many of the specimens closely resemble the figures of the Hardraw material given by Phillips, none of them shows "the striae being minutely crossed by lines of growth" as described and figured by Phillips, and hence there is some doubt that they are conspecific with *C. hardrensis*.

I have doubtfully referred the present specimens to *Rugosochonetes* on the very unsure foundation of the observation of weak concentric ornament on some specimens and a general resemblance in form to certain species assigned to the genus by Sokolskaya (1950).

In its pauci-striate ornament there is resemblance to some species doubtfully assigned to *Plicochonetes* by Paeckelmann (1930) but the ornament of our species is definitely striate and not plicate as in *P. buchiana* (de Koninck), the genotype of *Plicochonetes*, and also the internal structure of the brachial valve is much less complex.

It is probable that a new genus will have to be erected to embrace species of this type, but unfortunately the material at hand is not sufficiently well preserved to stand as genotype material.

EXPLANATION OF PLATE 14

(All specimens natural size and from Watts, Babbinboon unless otherwise stated. Specimen numbers refer to the University of New England Collections.)

FIG. *1–9—Unispirifer striatoconvolutus* (Benson & Dun). *1–4*, internal views of four pedicle valves showing variation in the conformation of the muscle field, F. 2501, F. 2522, F. 2485 and F. 2515 respectively; *5*, the pedicle cardinal area showing the vertical grooving, F. 2492; *6,7*, two pedicle valves, F. 2532 and F. 2483; *8,9*, two brachial valves, F. 2508 and F. 2533. (p. 68)

10–15—Brachythyris pseudovalis, n. sp. *10a-c*, ventral, dorsal and anterior views of a juvenile specimen, F. 2155; *11,12*, internal views of two pedicle valves showing the arrangement of the muscle scars; note the elongate adductor platform, F. 2180 and F. 2170; *13*, holotype dorsal view of a crushed specimen, F. 2183; *14*, a slightly incomplete pedicle valve, F. 2165; *15*, a brachial valve, F. 2186. (p. 76)

Range.—As yet *Rugosochonetes* has not been recognised outside of the Upper Devonian and Lower Carboniferous. During the latter period its distribution is world wide.

RUGOSOCHONETES? WERRIENSIS, n. sp.
Pl. 12, fig. 27–30

Holotype.—F. 2869 University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The pedicle valve has its greatest width at the hinge line and the outline of the valve is transverse. The cardinal extremities are acute and there is in some specimens a suggestion of mucronation. The central portion of the valve is strongly convex and there is a gradual change of slope onto the auriculations, which are much flatter. The venter is evenly rounded, there being no suggestion of a sinus. There are four to six spines along the cardinal margin on each side of the umbo. The cardinal area is low. The surface is ornamented with low rounded costae, of which there are eight to nine per 3 mm. near the anterior margin of the valve, and from 28–40 around the margin of the valve. There is a marked tendency toward smooth umbones, and costae also appear to be absent on the auriculations though this could be due to poor preservation. Very faint concentric ornament has been occasionally observed.

The brachial valve is strongly concave and follows the contour of the pedicle valve rather closely. The umbo is insignificant. There is a clear differentiation of the auriculations from the body of the valve.

Interior: Immediately beneath the pedicle umbo is a small, but sharp, median septum which divides the adductor scars. These are very narrow, together being only ½ to ¾ mm. wide in adult specimens, and are poorly defined. The diductor scars are much broader, distinctly impressed and rounded anteriorly. The interior surface is ridged and papillose.

The brachial valve has a small cardinal process from the base of which two low rounded ridges swing out in a slightly arcuate fashion at a low angle to the hinge. They become progressively more obscure laterally and are indistinguishable half-way to the margin of the valve. Separated from the base of the cardinal process and these ridges by a marked depression, are the adductor scars which are on slight platforms. In one specimen the adductor platform is raised into a septum-like structure anteriorly, but a true septum has not been observed. The outer edges of the adductor platform may be slightly raised to form two short diverging ridges. The whole interior surface, except the ears and the cardinal region, is crossed by strongly papillose ridges.

Dimensions (mm.).—

Pedicle valve

Length	Width at hinge	Height	Length of muscle field	Width of muscle field
8½	15	3½	2½	5
7½	11	2¾	—	—
7½	11	3	—	—
7½	13½	2½	—	—
7	13½	3	—	—
7	12	2½	2½	4½
5½	10	2	—	—

Brachial valve

Length	Width at hinge	Length of muscle field	Width of muscle field
7½	13½	2	2
7	13	3	3½
7	13	1¾	2

Remarks.—In the American Mississippian there are several strongly convex chonetids with coarse ornamentation, but only one, *Chonetes glenparkensis* Weller from the Glen Park and Chouteau limestones, has the extended hinge line and contour of *R.? werriensis*, n. sp. The figures of Weller (1914, pl. 8, fig. 47–49) show the striae becoming obsolete on the umbo, and the description indicates concentric ornament of the *Rugosochonetes* type. Unfortunately internal details are lacking.

The German Viséan species, *C. kayseri* Paeckelmann, is similar to *R.? werriensis* in form and size but has slightly coarser ornament.

None of the species described from Russia closely resembles *R.? werriensis*.

Range.—Upper Tournaisian; known only from the type locality.

Superfamily SPIRIFERACEA Waagen, 1883
Family SPIRIFERIDAE King, 1846
Subfamily SPIRIFERINAE Schuchert, 1913
Genus UNISPIRIFER, n. gen.
Genotype: *Spirifer striatoconvolutus* Benson & Dun, 1920

Diagnosis.—This genus is erected to include Spiriferidae in which the hinge-line is elongate and the cardinal extremities frequently mucronate during part or whole of the ontogeny. The lateral slopes bear costae the greater number of which are simple but some of which divide. In the sinus the costae are relatively few in number, consisting of a median which may be simple or bifurcating, flanked by the primaries which arise at the umbo. Only the median and primary costae originate on the umbo, and none are intercalated between the primary and median costae. The surface is finely striate.

Internally the pedicle valve is thickened in the umbo, and the free portion of the dental lamellae is short and wedge shaped, but in some cases the dental lamellae may be completely embedded in the umbonal thickening. The inner margins of the socket plates are carinate and they are not supported by plates reaching to the floor of the valve. The descending lamellae are developed from the socket plates.

Remarks.[1]—As thus defined this genus will include such European species as *S. tornacensis* de Koninck and *S. clathratus* McCoy, the American species *S. forbesi* Norwood & Pratten and *S. vernonensis* Weller and probably such Russian species as *S. baiani* Nalivkin.

George (1954, p. 314) has referred spiriferids of the *tornacensis* group to the genus *Cyrtospirifer*. This to me is a retrograde step for two reasons. First, this group can be readily distinguished from the *Cyrtospirifer* group on the basis of the nature of the costae in the sinus and on the lateral slopes; and second although there is a limited stratigraphical overlapping of the two groups, by and large *Cyrtospirifer* is typical of the Upper Devonian and *Unispirifer* of the Lower Carboniferous.

In species of the *Cyrtospirifer—Sinospirifer* group the sinal costae are always numerous (seven or more in adults) and in most species two or more pairs of costae originate in the umbo. A median costa may or may not be present, this feature being variable even within a single species; e.g., *Sinospirifer siniensis* (see Tien, 1938, p. 115). Costae may be intercalated between the primary costae later in ontogeny (see Maxwell, 1951, p. 7). The costae on the lateral slopes are invariably simple. In *Unispirifer* the sinal costae are fewer in number, always include a median costa, have no costae intercalated between the primary costae and have only one pair of costae (together with the median) arising on the umbo. The costae on the lateral slopes are variable in form even within the one species. For example in the species *U. striatoconvolutus* (Benson & Dun) some specimens exhibit simple costae only, while in others up to seven may bifurcate. Finally the cardinal area of the pedicle valve of *Unispirifer* is crossed by deep irregular grooves, which are never present on specimens of *Cyrtospirifer*, the cardinal area of which is ornamented by fine regular striae.

The Copenhagen Congress of the Comission on Zoological Nomenclature has ruled that a neotype must be a specimen similar to the original type and collected from the same locality. Since Martin's type of *Spirifer* has been lost, the application of this rule will mean that the neotype will be a specimen similar to that figured by Martin. *Spirifer* sensu stricto, thus has a hinge line shorter than the maximum width of the valve, a multicostate fold and sinus and a triangular area. These features are sufficient to distinguish it from *Unispirifer*.

Nalivkin (1937, p. 157) has erected the

[1] Since this paper was submitted for publication, the work of Glenister on the Upper Devonian and Lower Carboniferous spiriferids of the North-West Basin of Western Australia, has become available. A new genus *Austrospirifer*, with *A. variabilis* Glenister as genotype, has been erected. This genus may be distinguished from *Unispirifer* by its invariably simple lateral plications, the absence of "denticle grooves" (Glenister, p. 48) on the cardinal area of the pedicle valve, and by its peculiar glubose dental sockets.

The species referred to *Spirifer flexuosus* Glenister appears to be a member of *Unispirifer*.

Reference: GLENISTER, B. F., 1955, Devonian and Carboniferous spiriferids from the North-West Basin, Western Australia: Royal. Soc. West. Australia, Jour., vol. 39, pt. 2, p. 46–71, pl. 1–8.

genus *Imbrexia* with *Spirifer imbrex* Hall as genotype. This species has a general form and costation similar to *Unispirifer* but its surface is lamellose and non-striate.

Prospira, a Lower Carboniferous genus from the Mount Morgan region of Queensland was considered by Maxwell (1954, p. 35) to be a close relative of *Sinospirifer*. From *Unispirifer* it is readily distinguished by its coarser more rounded costae, poorly costate fold and sinus, weaker dental lamellae, and smaller size.

The Middle and Upper Carboniferous genus *Brachythyrina* Fredericks resembles *Unispirifer* in form, and in the costae on the lateral slopes, which are usually simple but may bifurcate, and in the costation of the sinus. However in the pedicle valve the plates supporting the teeth are reduced to thickenings along the edges of the delthyrium. Also, although fine concentric lamellae are recorded on members of this genus (e.g., de Verneuil [1845] and Chao [1929, p. 62]) there appears to be no record of striae.

Range.—This genus appears to be restricted to the Tournaisian during which time it attained an amazingly wide geographical distribution. In western Europe where it is represented by the *Spirifer tornacensis—Spirifer clathratus* group, it characterises the Middle and Upper Tournaisian. In Russia, Rotai (1931) has recorded *S.* aff. *S. tornacensis* from the C_1^2 beds (Upper Tournaisian) of the Donetz basin and Nalivkin (1937) has described *S. baiani*, which from the description and figures is closely related to *Unispirifer*, from the Rusakov limestones (Upper Tournaisian) of Northeast Kazakhstan. Sarycheva & Sokolskaya (1952) record the presence of *S. tornacensis* and related species from the lower part of the Tournaisian of the Moscow Basin. Frech (1899) records *S. tornacensis* from the Tournaisian of the Russo-Armenian and Persian border. In Kashmir the species recorded by Diener (1915) from the Syringothyris Limestone as *Spirifer* sp. ind. (cf. *bisulcatus* Sowerby) may be a member of the genus, as also may be the *S. tornacensis* de Kon. var. of Reed (1927) from Yunnan. From the Jumonji Stage (Upper Tournaisian) of the Kitakami Mountains of Honsyû, Japan, Minato (1952) has described a species, *Spirifer kozuboensis*, which belongs to *Unispirifer*. The American *Spirifer forbesi* Norwood & Pratten from the Osagean is a member of the genus.

UNISPIRIFER STRIATOCONVOLUTUS (Benson & Dun)

Pl. 14, fig. 1–9; Text-fig. 10a,11,12

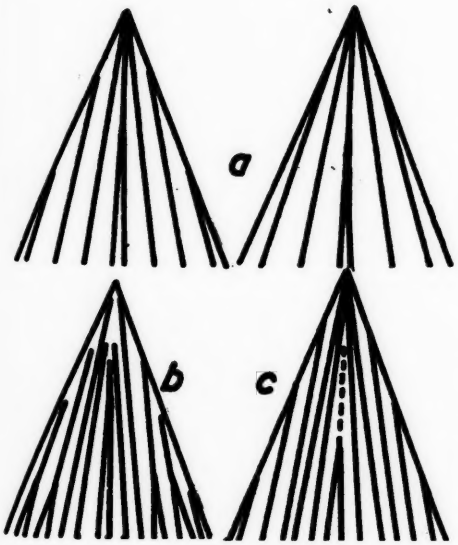
Spirifer striato-convoluta BENSON & DUN, 1920, Proc. Linn. Soc. New South Wales, vol. 45, no. 179, p. 350, pl. 20, fig. 7,8.

Holotype.—Specimen labelled F. 12461, Museum of the Geological Survey of New South Wales, and figured by Benson & Dun 1920, pl. 20, figs. 7,8. The locality given for this specimen is "Shelly Ridge in the S.E. of Babbinboon," and is undoubtedly, Watts, Babbinboon. (The type material in the palaeontological collections of the Geological Survey of New South Wales is at present being reorganised in the Australian Museum, and this specimen has not been available to me. The following description is based entirely on topotype material.)

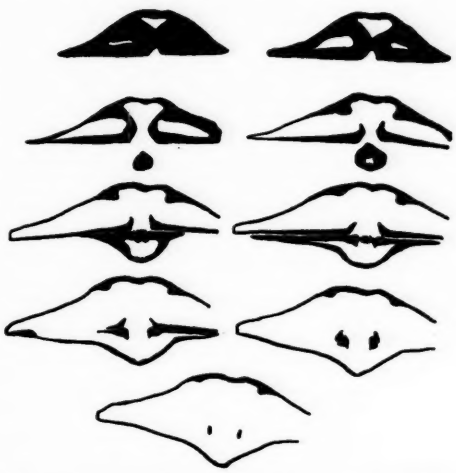
Description.—Exterior: The pedicle valve is most strongly convex in its posterior half. Its outline is alate and in adults varies from subtriangular to subsemicircular, and it also varies tremendously with age. The hinge line is very extended and long narrow mucros occur in juvenile forms. From juvenile to adolescent stages increase in width is accompanied by a proportionate increase in length, but beyond the adolescent stage (i.e., beyond a width of approximately 55 mm.) increase in length proceeds with relatively minor increases in total width. The relative length of the mucros tends to be reduced throughout ontogeny. The umbo is small, sharply pointed and slightly incurved. The cardinal area is rather high and subtriangular, but with abruptly terminated extremities. Its surface is traversed by a series of slightly irregular grooves which are partially filled with shelly material. The delthyrial angle averages 60°. The apex of the delthyrium is covered by a small, distinctly convex pseudodeltidium. The cardinal ridges are sharply angular and are concave toward the umbo but flatten out laterally. The median sinus is distinct and well defined but rather shallow. The sinal angle averages 15°. The lateral slopes are gently convex toward the

sinus but flatten out and become gently concave onto the ears. Ornament consists of costae which bear very fine striae. On each of the lateral slopes there are up to 30 rounded costae which are most frequently simple but which occasionally bifurcate. The sinus bears a median costa which reaches to within a few mm. of the umbo, and which becomes very broad and may bifurcate anteriorly. It is bordered on either side by two costae which arise either on the umbo or from the costae bordering the sinus at a distance of 2 or 3 mm. from the umbo (Text-fig. 10,a). Irregularly spaced growth lines occur over the whole surface.

The brachial valve varies in outline in a manner similar to the pedicle valve. The umbo is obtuse and rises well above the hinge line. A parallel-sided cardinal area is well developed. The lateral slopes are variable from slightly concave to slightly convex. The median fold is well defined by depressions which are broader than any of the inter costal depressions. The fold is rather low and scarcely breaks the general contour of the valve but it produces a marked flexure of the commissure. The costae on the lateral slopes are similar in type and number to those on the pedicle valve. The fold bears a median depression over most of its length, but anteriorly a low costa is usually developed within it. Lateral to this depression are three costae two of which are developed within 5 mm. of the umbo, but the third is developed at 20 mm. from the umbo.



TEXT-FIG. *10*—The arrangement of the sinal costae in, *a*, *Unispirifer striatoconvolutus* (Benson & Dun), compared with that of, *b*, *Cyrtospirifer verneuili* var. *grabaui* Paeckelmann and, *c*, *Sinospirifer siniensis* Grabau.



TEXT-FIG. *11*—Serial sections through the umbo of *Unispirifer striatoconvolutus* (Benson & Dun). ×0.6.

Interior: The pedicle valve is strongly thickened in the umbonal region. The dental lamellae are deeply embedded in the umbonal thickening and their free portions are short, thickened and wedge shaped. The arrangement of the skeletal material in the umbonal region is illustrated in Text-fig. 12. The muscle field is clearly defined. It is divided posteriorly by a short triangular callus from which arises a very low narrow and sharp median ridge which extends between three-quarters and the whole length of the field. On either side is a narrow adductor scar which increases slightly in width anteriorly, and which is situated on a low platform. The diductor scars are depressed and are pointed anteriorly. Their surface is longitudinally striated. The outline of the muscle field is variable but in general is broadly lenticular.

The brachial valve has very long dental sockets which reach up into the umbo. The inner edge of each socket plate is greatly thickened in the umbo and anteriorly this

thickening develops into a marked carina from which the descending lamellae of the spires are produced. No specimen with the spires in place has been found, but from several sectioned specimens it appears that no jugum is developed and spires with sixteen to twenty volutions are directed toward the cardinal extremities. In the umbonal portion is the cardinal process which consists of a shelly plate with its ventral surface deeply divided into up to 25 tiny vertical plates. It is supported laterally by the thickened edges of the socket plates. The adductor scars are poorly defined and are situated in small, shallow, elongate depressions on either side of the median fold, immediately in front of the socket plates. There is usually a faint, short, sharp median ridge present.

Dimensions (mm.).—

Pedicle valve					
Length	Width	Length of the muscle field	Width of the muscle field	Distance from the umbo to the anterior edge of the muscle field	Maximum width of adductor scars
33	64	12¼	11½	18½	—
32	58–	12	11½	17	1½
32	—	16	11	19	2½
30	70	11½	12	17	—
30–	—	13¼	11	18	—
29	58–	12½	12	13	1½
28	57–	11	9½	13	1½
28	67–	11	9½	13½	2¼
28	54–	10½	8½	14	1½
27	—	11½	9	15	2½
26	55–	9½	9	14	1¼
26	—	9	7	13	1½
25	50–	8½	5½	12½	1¾
23	52	9	11	11½	2

Remarks.—The youthful stages of this species are very mucronate, and even without the mucros the valves are very transverse in outline. As a general rule the relative length of the mucros decreases during ontogeny. It is unfortunate that the ears of adult specimens are in most cases not preserved, but in the best preserved specimens no mucros are present. Coupled with this change is an ontogenetic reduction in the length/width ratio. This ratio remains approximately constant until a width of 50–60 mm. is reached, when it rapidly increases (Text-fig. 14). One interesting feature brought out by this graph is the small range of variation in the length/width ratio in juvenile and adolescent specimens and its much wider range in adults.

Benson & Dun (1920, p. 350) in the original description of this species made a point of the "rather sinuous character of the ribs," but sinuosity is rare in the collections from this locality (the type locality) and can be regarded only as a minor variation within the population. These authors also remark on the symmetry of the costae on the lateral slopes. It should be noted that minor asymmetry is the rule rather than the exception, since it is only rarely that symmetrically placed costae on either side of the fold or sinus bifurcate. One of the most marked asymmetrical examples is figured on (Pl. 14, fig. 9). On this specimen the first seven costae on one side of the fold bifurcate at a distance of approximately 10 mm. from the umbo, but on the other side only one of the first seven bifurcate.

The specimen figured by Weller (1914, pl. 42, fig. 1–3), as *S. forbesi* Norwood & Pratten is similar in outline to some specimens of *S. striatoconvolutus* but it is too elongate to be typical of that species. The costae of the fold and sinus differ slightly in that the median costa of the sinus does not broaden and bifurcate and no median costa is inserted on the anterior portion of the dorsal fold. *Spirifer platynotus* Weller (1914, pl. 39, fig. 1–10) is almost identical externally with the adolescent stages of *S. striatoconvolutus*. This is the only species with which I am acquainted which has sinal

TEXT-FIG. *12*—A diagrammatic sketch of a section through the pedicle umbo of *Unispirifer striatoconvolutus* (Benson & Dun) showing the arrangement of the calcite fibres within the shell. ×2.

and fold costae identical with those of *S. striatoconvolutus*, but it never appears to attain the size of this latter species. Unfortunately its internals have never been described.

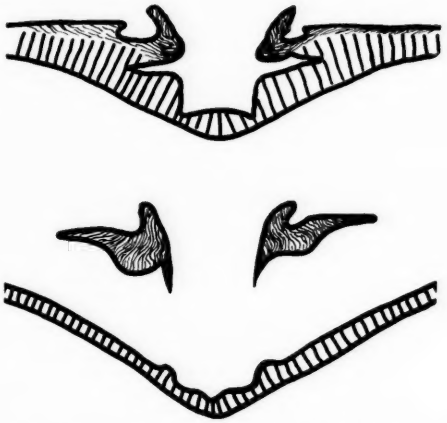
In the ontogenetic variation of its form, the ornament of its lateral slopes and the internal structure of its pedicle valve *S. tornacensis* resembles *S. striatoconvolutus*. There are however slight differences in the costation of the fold and sinus. The former is well illustrated by the specimen from Tournai figured by Vaughan (1915, pl. 6, fig. 4). Some of the specimens referred to *S. clathratus* McCoy are closely comparable with the present species, e.g, the specimen figured by Vaughan (1905, pl. 26, fig. 5) from the Z_1 zone of the Avon Gorge sequence.

In the Donetz Basin on an horizon equivalent to the English Z_2, Rotai (1931) has found a species very similar to the young forms of *S. striatoconvolutus* which he has referred to *S.* aff. *S. tornacensis* de Koninck.

Range.—In New South Wales this species has been found in rocks of the middle and upper portions of the Lower Burindi Group which are thought to represent the Middle and Upper Tournaisian.

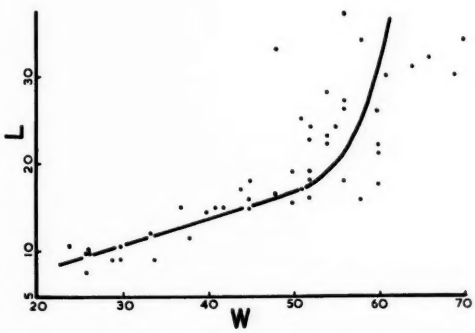
Genus ECTOCHORISTITES, n. gen.
Genotype: *Ectochoristites wattsi*, n. sp.

Description.—The valves are subequally biconvex and the hinge is approximately equal to the maximum width of the shell. Beyond a certain growth stage increase in the length of the shell is not accompanied by increase in the width of the hinge but does produce a higher cardinal area. As a result, the cardinal area of adults is laterally



TEXT-FIG. *13*—Diagrammatic sketches of two sections through the umbo of the brachial valve of *Unispirifer striatoconvolutus* (Benson & Dun), showing the arrangement of the calcite fibers. ×4.

truncated. The shell material of the cardinal area is deeply grooved transversely in the manner described above for *Unispirifer*. The costae of the lateral slopes frequently bifurcate. The fold and sinus are multicostate some of the costae being simple and others bifurcating once or twice. Internally the dental lamellae are short thick wedge shaped structures, the development of which is illustrated in Text-fig. 18. The descending lamellae of the brachia are derived from the carinate inner edges of the socket plates. These plates may reach the floor of the valve for a very short distance beneath the umbo.



TEXT-FIG. *14*—Scatter plot of the ratio length /width of the pedicle valves of *Unispirifer striatoconvolutus* (Benson & Dun).

Remarks.—This genus bears a superficial resemblance to *Choristites* but it may be readily differentiated on the basis of internal structures. In *Choristites* the dental lamellae are in juxtaposition in the umbo, they are very elongate and are subparallel throughout their length, whereas in the present genus they do not exist as separate structures in the umbo and they are short and divergent. The genus *Yatsengina* Semichatov is similar to *Choristites* in most respects and can be distinguished from *Ectochoristites* by the same features. Neither of these genera occur below the base of the Middle Carboniferous.

The Lower Carboniferous genus *Eochoristites* described by Chu (1933) from the Kinling limestone is somewhat similar to *Ectochoristites* in form and in such internal structures as the curved divergent dental lamellae (which are much shorter than those of *Choristites*), and the crural plates of the brachial valve, but the structural details are quite dissimilar. *Eochoristites* has a triangular area which is marked only by horizontal striations; the costae of the lateral slopes are invariably simple; the costae in the sinus are few in number in comparison with *Ectochoristites* and they never bifurcate; the ends of the dental lamellae are wedged into the shell wall as in *Choristites*; the "apical" plates of the brachial valve are apparently invariably present and are up to 5 mm. long whereas in *Ectochoristites* they are only up to 1 mm. long and in some cases are completely eliminated by the thickening of the umbo.

Sokolskaya (1941) erected the genus *Palaeochoristites* to cover certain Tournaisian species from the Moscow basin which are transversely oval in outline, and have a hinge line slightly shorter than the greatest width of the shell, lateral slopes with many simple costae and dental lamellae which are high and straight and extend from one third to one half the length of the shell. This genus, then, can be separated from *Ectochoristites* by its triangular cardinal area, simple costation and elongate *Choristites*-like dental lamellae.

From *Cyrtospirifer* it may be distinguished by its truncated area, shorter hinge and finer bifurcating costae on the lateral slopes, as well as the lack of surface striation.

Reed (1948) has described from Fife a group of specimens which he refers to Fredericks' genus *Brachythyrina*. These species are similar to *Ectochoristites* in external form of the pedicle valve, the truncated cardinal area which is transversely grooved and the presence of short, thick dental lamellae supporting excavate teeth; but they differ in the fewer, coarser costae on both the lateral slopes and the sinus and fold. Their reference to *Brachythyrina* appears to be incorrect since that genus usually has a wider hinge, and no dental lamellae. Reed notes several points of similarity to *Eochoristites* which genus they homeomorph rather closely. Unfortunately the internal structures of the Fife specimens are not adequately described for detailed internal comparisons to be made, but externally *Eochoristites* can be distinguished by its simple lateral ribs and its triangular area without transverse grooves. The Fife specimens thus appear to be most closely allied to *Ectochoristites*.

Other British forms probably belonging to this genus are those figured by Davidson (1857, pl. 4, fig. 13,14) which he refers to *Spirifer mosquensis* Fischer. In his description the normal internals of *Choristites* are described but later (p. 22) he remarks that

> The very few British examples of this species which I have been able to examine did not present any interior, but the external characters are so exactly similar to some Russian examples . . . that I have felt no doubt as to their identity.

To my knowledge no true *Choristites* has been found in Dinantian rocks and there is a high probability that the *S. mosquensis* of Davidson will be found to have the internal structure of *Ectochoristites*. *Unispirifer* is very similar to *Ectochoristites* in internal structures and in its high cardinal area with truncated extremities, but differs in its coarser costae, much less costate fold and sinus and its much longer hinge-line.

The genus *Spirifer* has a different mode of growth, the ratio of the width of the hinge to the total length remaining approximately constant throughout ontogeny. This results in a simple triangular cardinal area whereas in *Ectochoristites* that structure is triangular only until the late adolescent stage is reached, after which the extremities become truncated.

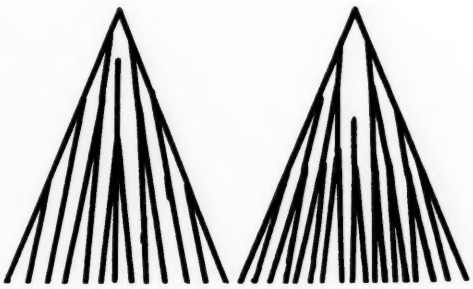
Range.—So far as is at present known, this genus is restricted to the Lower Carboniferous. In Australia it has been found only in the upper parts of the Lower Burindi Group of Upper Tournaisian age; in America it is apparently restricted to the Kinderhookian and Osagean; in Ireland it may be present in the Charlestown limestone which is Upper Viséan or perhaps Lower Namurian.

ECTOCHORISTITES WATTSI, n. sp.
Pl. 15, fig. 1–7; Text-fig. 15–21

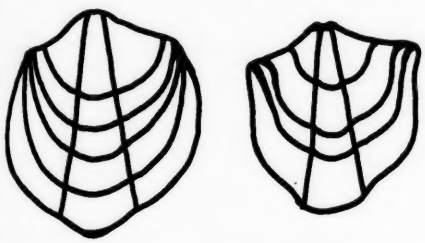
Spirifer cf. *mosquensis* (Fischer). BENSON & DUN, 1920, Proc. Linn. Soc. New South Wales, vol. 45, no. 179, p. 348, pl. 20, fig. 4–6.

Holotype.—F. 1868, University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

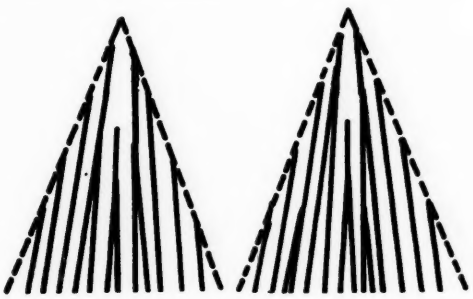
Description.—Exterior: The pedicle valve is strongly convex particularly toward the umbo, but it flattens out over the central and anterior portions. This imparts a pigeon-chested appearance. In some specimens the greatest width is at the hinge and the outline is subsemicircular whilst in others the hinge is less than the maximum width and the outline more elongate. The outline also varies with age as can be readily seen from Text-fig. 15. The width of the hinge increases approximately proportionately to the length until the width reaches 22–32 mm., beyond which there is a rapid increase in the length/width ratio, and new growth adds to the height of the cardinal area but not to the width of the hinge. In general the outline during ontogeny varies from subtriangular in juveniles, sometimes with mucronate cardinal extremities, to subsemicircular with subrectangular cardinal extremities. In most specimens most of the area is slightly concave but it becomes more strongly concave immediately beneath the umbo. Its surface is transversely marked by fine irregular grooves which in adult forms may number up to thirty on each side of the delthyrium. The delthyrium itself is broad and open, the delthyrial angle averaging 54° (range 51°–58°). The umbonal slopes are sharp. The median sinus is well defined on the posterior portion of the valve but its margins become increasingly vague toward the front where it is produced into a high rounded lingual extension. The sinal angle is very variable, ranging between 11° and 29° (average 20°). The lateral slopes and sinus are finely costate with twenty-five to thirty costae on each of the lateral slopes and up to twenty in the sinus of adult specimens. The costae on the lateral slopes frequently bifurcate on the posterior quarter of the valve, but divide only rarely over the remainder of their length. The basic sinal patterns are illustrated in Text-fig. 16. There are variations, not always symmetrical, upon this scheme, particularly in specimens with a



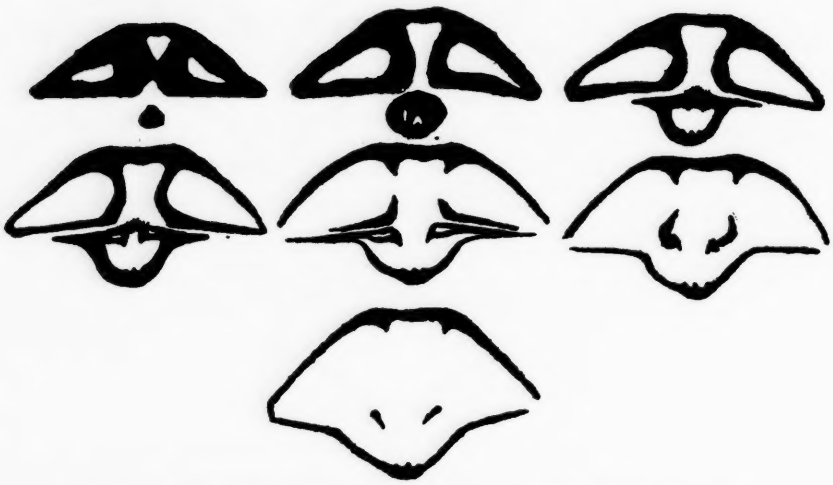
TEXT-FIG. *16*—Diagrammatic representation of some of the costal patterns in the sinus of *E. wattsi*, n. sp.



TEXT-FIG. *15*—Variation in the outline of the pedicle valve of *E. wattsi*, n. sp. during ontogeny. ×0.7.



TEXT-FIG. *17*—Diagrammatic representation of some of the costal patterns on the fold of *E. wattsi*, n. sp.



TEXT-FIG. *18*—Serial sections through the umbo of *E. wattsi*, n. sp. ×1.

wide sinus. The variation usually consists of irregular bifurcation of costae on the anterior part of the valve.

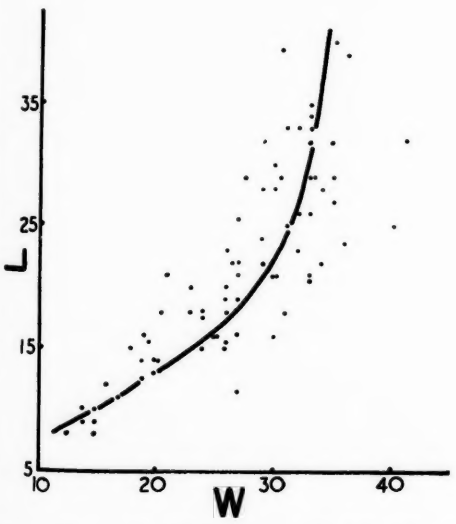
The brachial valve is almost semicircular in outline, but as with the pedicle valve, it too varies considerably during ontogeny. The maximum width is almost reached by the time the valve is three-quarters of its adult length. In anterior profile the valve is subtriangular the median fold scarcely breaking the contour. The fold is outlined by depressions somewhat larger than those separating the costae. The umbo is small and slightly elevated. The cardinal area is well developed and more or less parallel sided. The costae on the lateral slopes are similar in type and disposition to those on the pedicle valve. The arrangement on the fold is variable, some of the variants being represented in Text-fig. 17.

Interior: The pedicle valve bears short, thickened, wedge-shaped, diverging dental lamellae whose structure can be seen in Text-fig. 19. The teeth are borne on the folded portion of the shell wall and not upon the tissue which forms the inner lining of the lamellae. The teeth are large hooked structures which project inwards and upwards to the sockets. The dental lamellae are not planar. The tooth bearing portions (dental lamellae of Browne, 1953) converge inside the delthyrium but then diverge again toward the outer margin of the shell (forming the adminicula of Browne). These two portions do not form separate plates which are sutured together as Browne has suggested in the case in *Martiniopsis*, but are in fact structurally continuous. Thickening of the shell invariably occurs inside the apical portion of the delthyrium. The adductor scars are very long and narrow, usually extending to the mid-point of the shell. They are divided over their posterior half by a low but sharp ridge which becomes progressively less distinct anteriorly. The diductor scars are very variable in width so that the outline of the whole muscle field varies from almost

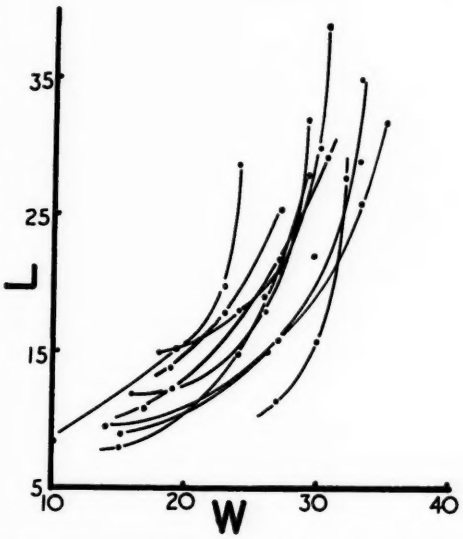
TEXT-FIG. *19*—Diagrammatic representation of sections through the umbo of *E. wattsi*, n. sp., to illustrate the arrangement of the calcite fibers. ×1.9.

subcircular to an elongate ellipse. Ovarian pits are usually poorly developed but in some adults they can be seen immediately on each side of the delthyrium and posterolaterally to the muscle field.

In the brachial valve the socket plates are much thickened and they unite beneath the umbo where they support the cardinal process on their outer surface. The sockets are completely enclosed for most of their length. The cardinal process is a broad structure composed of up to twenty-five separate plates. Two plates, up to 1 mm. in length reach to the floor of the valve in the umbo and support the inner edges of the socket plates. These plates are one with the socket plates and are formed by secretion of excessive calcite at their inner edge, as can be seen from Text-fig. 18. The long straight descending lamellae are produced from the inner edges of the socket plates. The margins of the fold are marked by two low rounded ridges, which are continuous with the plates in the umbo. A low median septum which reaches a maximum height of 1 mm. arises in the thickening of the umbo and tapers to the mid-length of the valve. Although this septum is not very high it is a much larger and more significant structure



TEXT-FIG. *20*—Scatter diagram of the length /width of hinge ratios of the pedicle valves of *E. wattsi*, n. sp., showing the trend of the whole population.



TEXT-FIG. *21*—Scatter diagram of length/width of hinge ratios of the pedicle valves of several specimens of *E. wattsi*, n. sp., showing individual ontogenies.

than the narrow ridge which separates the adductor scars in such genera as *Unispirifer*. The adductor scars are long and narrow and very indistinct.

Dimensions (mm.).—The length/width ratios of the pedicle valves are reproduced in Text-fig. 20.

Pedicle valves

Length	Width	Length of muscle field	Width of muscle field	Width of adductor scars
25	33	14	9	1½
29	31	16	8½	1¾
30	34	13	8½	1
31 ±	36	13½	14	2½
32	41	15½	7	—
34 ±	30	18	9	1
38	35	18	13½	—

Brachial valves

Length	Width	Length of median septum
20	27	9
20	33	12½
24	36	11
27	37	17
30	27	14

Remarks.—There is little to distinguish this species from *Spirifer gregeri* Weller

from the Chouteau limestone of North America, apart from minor differences in proportion and the size of the costae. The internal structure, particularly of the brachial valve, of the Chouteau species has not been well described or illustrated, and further distinguishing features may become apparent on further study. The lateral costae of *S. gregeri* are broader than those of *E. wattsi*, n. sp., and the sinal costae are less numerous and exhibit minor differences in arrangement.

The species from the Charlestown limestone of Fifeshire referred by Reed (1948) to *Spirifer* (*Brachythyrina*) Sowerby var. *roscobiensis*, and *Spirifer* (*Brachythyrina*) *bisulcatus* Sowerby, var. *acuticardinalis* are almost certainly members of this genus, but they differ from *E. wattsi* in their much broader lateral costae which bifurcate only on the anterior half of the shell, and in their more coarsely costate fold and sinus.

Range.—As yet this species is known only from the type locality—Upper Tournaisian.

Subfamily BRACHYTHYRINAE Fredericks, 1926

Genus BRACHYTHYRIS McCoy, 1844

Genotype: *Spirifera ovalis* Phillips

Remarks.—This genus has been adequately discussed recently by George (1927), Muir-Wood (1948) and Maxwell (1954).

BRACHYTHYRIS PSEUDOVALIS, n. sp.

Pl. 14, fig. 10–15; Text-fig. 22

Spirifera pinguis (Sowerby), BENSON & DUN, 1920, vol. 45, no. 5, p. 348, pl. 20, fig. 9,10.

Holotype.—F. 2183. University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: This species is unequally biconvex, the pedicle valve being much the more strongly convex. All specimens are wider than they are long.

The pedicle valve is most strongly convex toward the umbo. The umbo is sharp and strongly overhanging the cardinal area which is thus strongly concave. The area is between three and four fifths of the maximum width of the shell. Its surface bears a series of very closely set regularly spaced vertical striations, usually about 8 per mm. The delthyrial angle is approximately 45°. The delthyrium is largely covered by a vaulted pseudodeltidium. The median sinus is generally deep, reaches onto the umbo, and in almost all cases it is open V-shaped in section and bears a median furrow. The sinal angle ranges from 11° to 15°. The lateral slopes are evenly convex and each bears up to fourteen rounded plicae the two or three on the lateral extremities being usually very indistinct.

The brachial valve is suboval in outline. In lateral profile it is convex at the umbo and flat over the remainder of the valve, while in transverse section it is in the form of a very open inverted V (Text-fig. 22). The median fold is sharply defined by a change of slope and furrows. It is variable in height and form, occasionally being sharp on its crest but usually rounded. In some specimens a very faint furrow is borne medially upon it, but in others this feature is absent. The plicae on the lateral slopes are usually simple but irregularly arranged bifurcation has been observed on some specimens.

Interior: In the pedicle valve there is considerable variation in the degree of thickening of the shell in the umbonal region (pl. 14, fig. 11,12) and in the form of the muscle scars. In most cases the thickening is slight and the delthyrial cavity is shallow, but cases of heavy thickening with a deep triangular delthyrial cavity do occur. The muscle scars are situated in a shallow depression well forward from the umbo. The diductor scars are usually elongate and acuminate both posteriorly and anteriorly, and they are divided by a narrow depression, containing the adductor scars, which extends three to 6 mm. beyond their anterior extremity. This adductor depression is very narrow and its limits are usually poorly defined. All the scars are finely stri-

TEXT-FIG. *22*—Anterior view of an undistorted specimen of *B. pseudovalis*, n. sp.

ated longitudinally. In one specimen the diductors are very broad and asymmetrical. The teeth are large and are supported on heavy dental ridges which bound the inner margins of the delthyrium. These ridges never reach the floor of the valve.

In the brachial valve the socket plates are strong, enclosing large sockets, and their inner ventral edges bear high sharp carinae from which arise the flattened descending lamellae of the brachia. In all of the specimens available the spires are broken. The cardinal process is situated immediately beneath the umbo and is wedged between the socket plates. A very faint median ridge separates very indistinct adductor scars.

Dimensions (mm.).—

Length	Width	Height	Length of diductor scars	Total width of muscle field	Length of adductor scars	Height of fold
			Pedicle valves			
53	59	19–	—	—	—	13
—	55–	—	21	16	21	—
50	50	16–	—	—	—	9
46	56	—	—	—	—	—
44	57	16	—	—	—	—
42	51	16–	11	7	17–	—
39	46	12–	10	7	13–	7–
31	35	—	—	—	—	4
			Brachial valves			
37	—	—				8½
37	50	—				9
35	50	8				4½
—	52	8½–				8½
25	35	—				4

Remarks.—This form was referred by Benson & Dun (1920, p. 348) to *Spirifera pinguis* (Sowerby). Only two specimens (both pedicle valves) appear to have been available to these authors. From that species however it can be readily distinguished by the lack of the strong median furrow in the fold on the brachial valve.

De Koninck (1876, p. 185, English translation) has recorded the presence of a form which he refers to *Spirifera pinguis* (Sowerby) at Glen William and Burragood. This is the same species as that from Lewinsbrook which McCoy (1847) has referred to *Spirifera tasmaniensis* (Morris). I have examined specimens from both the Glen William and Lewinsbrook localities and am satisfied that they are conspecific and that they differ from *B. pseudovalis* in being consistently relatively broader, in having a much less prominent and less acute umbo, and slightly coarser plication of the lateral slopes.

Of the American species the closest comparison is with *Brachythyris suborbicularis* (Hall) from the Keokuk limestone of Iowa. As interpreted by Weller (1914) this species has a very broad range of variation which might well include forms of the *B. pseudovalis* type. The *B. suborbicularis* group in America is restricted to the Burlington and Keokuk limestones (Weller, 1914, p. 376; Wanless et al., 1948, correlation chart).

B. pseudovalis, n. sp., does not have the deeply plicated fold of *B. subrotundata* (McCoy) but in ornament, breadth of hinge and general conformation it closely resembles some of the specimens referred to that species by Davidson. From the *B. ovalis* (Phillips) group it is readily distinguished by the breadth of its hinge and the smaller width of its plicae. In Britain the *B. subrotundata—B. pinguis* groups, which are apparently closely related, are well developed in the Viséan but occur also in the Tournaisian.

Nalivkin (1937) has recorded *Brachythyris suborbicularis* (Hall) and the related *B. atbasarica* Nalivkin from the lower Viséan Ishim beds of northeastern Kazakhstan.

The species *B. kitakamiensis* Minato (1951) from the Hikoroiti Series of Honsyû,

thought by Minato to be equivalent of Zone d'Etroeungt, has fewer plicae on the lateral slopes than the present species.

Range.—This species is known at present only from the type locality, Upper Tournaisian.

Subfamily MUNELLINAE Fredericks, 1926
Genus STROPHOPLEURA Stainbrook, 1947
Genotype: *Spirifer notabilis* Kindle.

Diagnosis.—This genus includes small Spiriferidae which are very transverse in outline and have extended cardinal extremities. They are *Spiriferina*-like in form, the two folds bounding the sinus being disproportionately large. The valves are partly or completely lamellose. Internally the dental lamellae are short and a low sharp median ridge may be developed. Short plates may support the crural bases in the brachial valve. The shell is impunctate.

Remarks.—The ornament of the genotype is characterized by the large plicae bounding the sinus and the discordant plication of the lateral slopes which is so well illustrated in Kindle's figures. The degree of discordance in the type specimens is variable and is scarcely noticeable in the specimen figured by Stainbrook (1947, pl. 44, fig. 17–20).

The internal structure of the genotype does not appear to be satisfactorily known. Kindle gave no description of the interior. Stainbrook's diagnosis of the genus (p. 324) contains the ambiguous statement "no internal septa *noted* [my italics] in either valve." This is followed by a comparison with *Reticulariina* and *Tylothyris*, and from the former it is stated that *Strophopleura* differs "in having a non-septate pedicle valve," and from the latter "in lacking a median septum in the pedicle valve." Since both *Reticulariina* and *Tylothyris* have dental lamellae it would appear that *Strophopleura* has dental lamellae but no median septum. However, on p. 325 *S. notabilis* is considered to be similar to the *Delthyris novamexicana* (Miller) or Weller, "with which it appears to be congeneric," even though Weller (1914, p. 305) indicates that the muscle scars of the pedicle valve of *D. novamexicana* are

> divided longitudinally by an angular ridge which becomes more septum-like towards the beak, and which in young samples with less solidified beaks, perhaps became a distinct median septum.

EXPLANATION OF PLATE 15

(All specimens are from Watts, Babbinboon and are natural size unless otherwise stated. Specimen numbers refer to the University of New England Collections.)

FIG. *1–7—Ectochoristites wattsi* n. gen., n. sp., *1*, holotype, pedicle exterior, F. 1868; *2*, pedicle exterior showing variation in form, F. 1874; *3*, brachial exterior, also showing vertical grooving of the pedicle cardinal area, F. 1903; *4a,b*, lateral and anterior views of a complete specimen, F. 1902; *5,6*, molds of two pedicle interiors showing variation in the form of the muscle field, F. 1870 and F. 2845; *7*, mold of brachial interior, F. 2844. (p. 73)

8,9—Eumetria? mona, n. sp., *8a-c*, ventral, dorsal and anterior views of the plaster cast of a specimen used for serial sectioning, F. 2814; *9*, holotype, pedicle exterior, ×1.2, F. 2812. (p. 85)

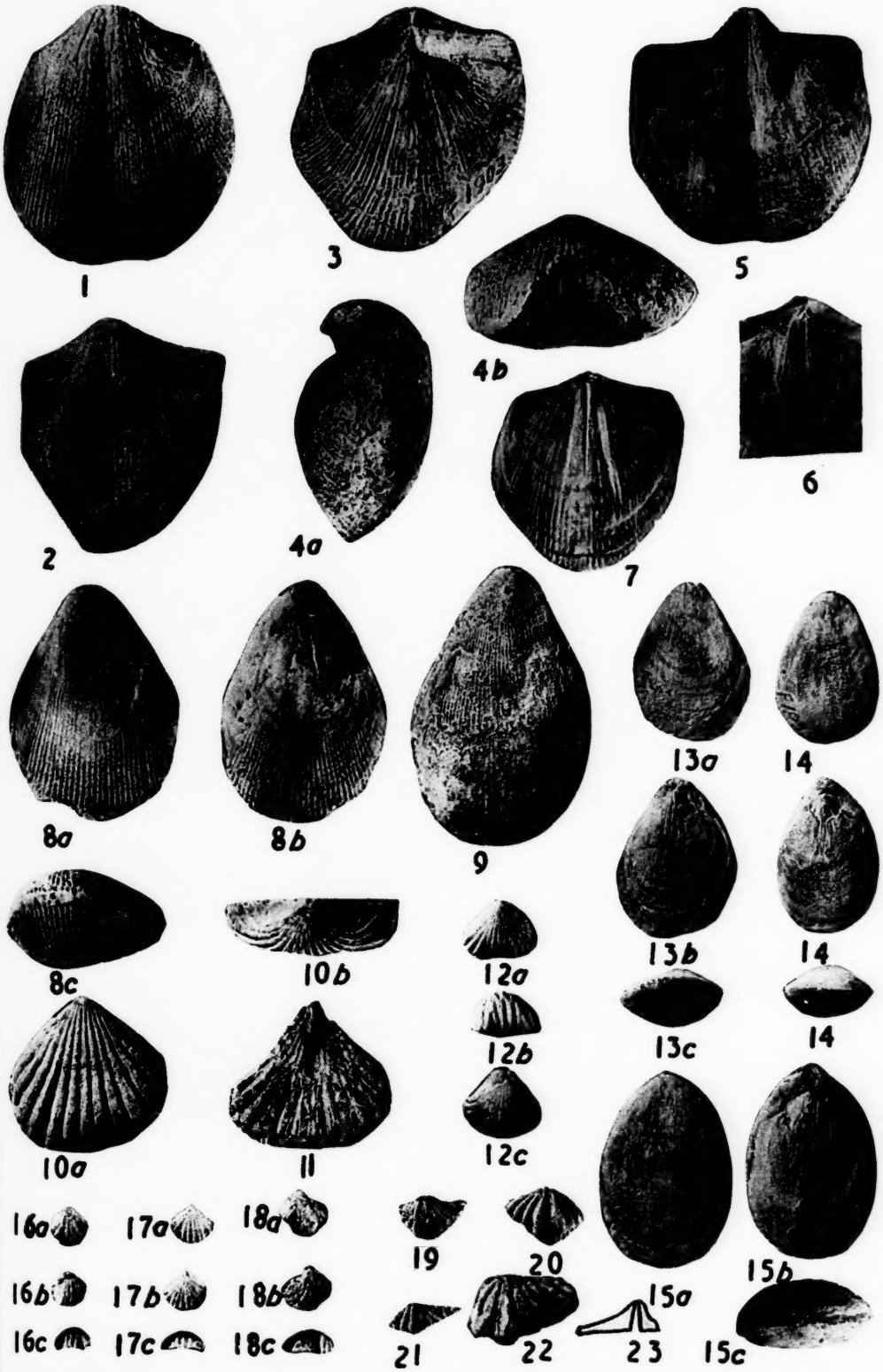
10,11—Tetracamera cf. *T. subtrigona* (Meek & Worthen). *10a,b*, ventral and posterior views of a pedicle exterior showing the flexed margins of the valve, F. 2710; *11*, a pedicle interior, F. 2711. (p. 89)

12—Camarotoechia sp. Ventral, anterior and dorsal views, F. 2823. (p. 90)

13–15—Balanoconcha elliptica n. gen., n. sp., *13a-c*, ventral, dorsal and anterior views, F. 1815; *14a-c*, ventral, dorsal and anterior views, F. 1820; *15a-c*, holotype, ventral, dorsal and anterior views, F. 2825. (p. 86)

16–18—Pugnax minutus, n. sp., *16a-c*, holotype, ventral, dorsal and anterior views, ×0.8, F. 2819; *17a-c*, and *18a-c*, the same views of two other specimens, ×0.8, F. 2820, and F. 2821. (p. 90)

19–23—Strophopleura anterosa, n. sp., *19*, holotype, pedicle valve showing lamellation, F. 2575; *20*, mold of pedicle interior; the median ridge is not nearly so pronounced as the photograph seems to indicate, F. 2574; *21*, brachial exterior, F. 2567; *22*, mold of brachial interior showing the short crural plates, ×2, F. 2577; *23*, sketch of pedicle interior, showing the trace of the dental lamellae on the cardinal area, F. 2576. (p. 79)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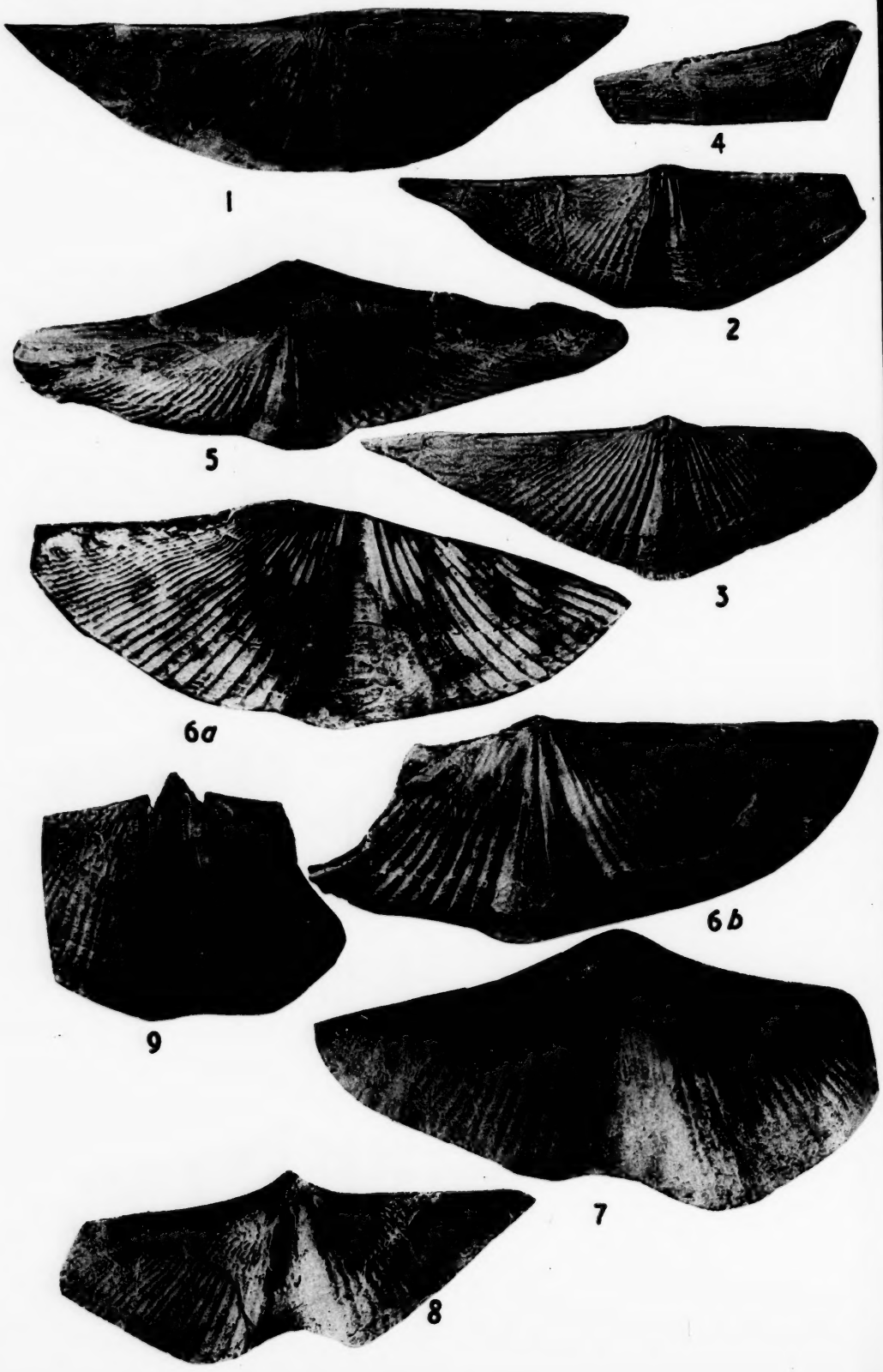
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No data are available on the internal structure of the brachial valve.

It is possible that *Spirifer mundulus* Rowley from the Burlington limestone of the Mississippi Valley is related to *Strophopleura* being similar to it in size and form and having enlarged plicae bordering the sinus. The surface however is only weakly lamellose, being "marked by rather faint concentric lines of growth which are somewhat crowded towards the front margin" (Weller, 1914, p. 333). The internal structures have not been described.

The species, *Strophopleura anterosa*, n. sp., is similar to *S. notabilis* in size, shape and the presence of the enlarged plicae bounding the sinus. Like *Spirifer mundulus* its lamellation is weaker than in *S. notabilis* and like the *Delthyris novamexicana* of Weller it has a low angular median ridge in the pedicle valve. Perhaps of greater significance is the presence of a system of grooves on the cardinal area of *S. anterosa* similar to those described previously on *Unispirifer* and *Ectochoristites*. These have not been described on *S. notabilis* whose area is "marked by faint vertical striations."

Range.—This genus up till the present has been recorded only from the Tournaisian rocks of North America.

STROPHOPLEURA ANTEROSA, n. sp.
Pl. 15, fig. 19–23

Holotype.—F. 2575. University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: This species is small and very transverse. The hinge line is at the greatest width of the shell and the cardinal extremities are sharply acute and may be slightly mucronate.

The umbo of the pedicle valve is prominent and the sharp umbonal ridges are deeply concave toward the umbo but rapidly flatten out toward the cardinal extremities. The cardinal area extends the whole width of the valve and is strongly concave. It is traversed by grooves similar to those seen in *Unispirifer*. The delthyrium is narrow, the delthyrial angle approximating 20°. A marked sinus which may be U- or V-shaped, and is produced into a high tongue anteriorly, is developed. On the tongue the sinus tends to flatten out and on one specimen the tongue is almost completely flat. Bordering the sinus on either side is a large plication which is much stronger than the adjacent ones on the lateral slopes. Each lateral slope carries five or six plicae including those bounding the sinus. The posterior half of the valve bears weakly developed lamellae, but the anterior portion has a region of variable width on which the lamellae are strongly developed. On some specimens this region is restricted to the margins but on others it occupies half of the valve.

The brachial valve is rather strongly convex. The umbo is small and obtuse. The median fold is high and rounded and separated from the lateral slopes by deep grooves. The lateral slopes bear four or five rounded plicae similar to those of the pedicle valve. A well developed parallel sided cardinal area is present.

Interior: The umbo of the pedicle valve is unthickened. Very short delicate subparallel dental lamellae occur in the apex of the umbo (1½ mm. long in a specimen of total length of 6½ mm.). The teeth are small. The muscle field is ellipitcal in outline, and its posterior end is situated be-

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EXPLANATION OF PLATE 16

(Specimen numbers refer to the University of New England Collections unless otherwise stated.)

FIG. *1–9*—*Asyrinxia lata* (McCoy). *1*, lectotype, mold of pedicle interior, ×1, E. 10643 Sedgwick Museum, Cambridge, locaiity Lewinsbrook, N.S.W.; *2*, mold of a pedicle interior of a younger topotype, ×1, F. 2577; *3*, mold of a brachial interior of a topotype, ×1, F. 2592B; *4*, mold of the cardinal area of a specimen from Hilldale, N.S.W., ×1, F. 2601; *5*, a distorted specimen from Clarencetown, ×0.9, F. 2578B; *6a,b*, molds of the exterior and interior of a brachial valve from Clarencetown, ×1, F. 2583*A*,B; *7,8*, molds of the interior of two pedicle valves from Clarencetown, showing variation in the umbonal thickening with age, ×1, F. 2580 and F. 2582; *9*, mold of part of the interior of a specimen from Watts, Babbinboon, ×1.3, F. 2579. (p. 81)

tween the tips of the dental lamellae. In one specimen 10 mm. in length the muscle field is 3 mm. long. A low sharp ridge is found between the scars.

In the brachial valve the sockets are very narrow and inclined at an angle of approximately 45° to the hinge. The socket plates are thickened and are supported on short crural plates which extend along the floor of the valve a distance of approximately 1–1½ mm. in adults.

The shell material is impunctate.

Dimensions (mm.).—

Pedicle valve

Length	Width	Height	Sinal angle
6	15	—	—
7	16±	4	20°
8	16±	—	25°
10	—	6±	20°

Brachial valve

Length	Width
5	17
4½	10±

Remarks.—This species is most nearly related to *Spirifer mundulus* Rowley, from which however it may be distinguished by its smaller size and fewer plications. *Strophopleura notabilis* (Kindle), too, is a larger more plicate species which also differs in its more marked lamellae, flatter cardinal area and much broader delthyrium. *S. mundulus* is found in the Lower Burlington limestones of Upper Tournaisian age.

Range.—This species is known so far only from the type locality, Upper Tournaisian.

Superfamily PUNCTOSPIRACEA Cooper, 1944
Family SPIRIFERINIDAE Davidson, 1884
Subfamily SPIRIFERININAE Schuchert, 1929
Genus PUNCTOSPIRIFER North, 1920

Punctospirifer NORTH, 1920, p. 212–4, pl. 13, fig. 6. DUNBAR & CONDRA 1932, p. 351–5, pl. 38, fig. 1–5. MUIR-WOOD 1948, p. 62–5, pl. 1, fig. 9; pl. 2, fig. 5–10,12.

Genotype: *Punctospirifer scabricostus* North.

Remarks.—This genus has been adequately discussed by the authors listed in the synonymy.

PUNCTOSPIRIFER sp.

Description.—Exterior: Only one pedicle valve is referable to this genus.

The shell is small (11 mm. in length). Its cardinal extremities are not preserved but from the juvenile stages it appears that they are subrectangular and slightly rounded. The sinal angle is approximately 25°. The lateral slopes bear seven or eight low rounded ribs. The cardinal area is low (about 4 mm. in height) and gently concave, and the delthyrial angle is approximately 40°. The shell material is coarsely punctate and the surface of the shell is finely lamellose.

Interior: Short dental lamellae are developed. The median septum is high and reaches half of the total length of the valve.

Remarks.—This species is distinguished from the genotype by its lower cardinal area and larger delthyrial angle. *Punctospirifer subtextus* (White) from the Kinderhook and Burlington limestones of the Mississippi Valley is comparable with this form in all external features, but unfortunately nothing is known of its interior. There also appears to be a close resemblance to *P. malevkaensis* Sokolskaya from the Tournaisian beds of the Moscow basin.

Range.—This species is known only from Watts, Babbinboon; Upper Tournaisian.

Subfamily SYRINGOTHYRINAE
Fredericks, 1925
Genus ASYRINXIA, n. gen.
Genotype: *Spirifera lata* McCoy.

Diagnosis.—The shell is spiriferoid with an alate outline, and a high triangular pedicle cardinal area. The costae on the lateral slopes are simple and the sinus bears four or six weak costae which are restricted to its lateral portions. The pedicle cardinal area is characterised by a threefold division in its ornament as in *Syringothyris*. Strong dental lamellae are present. The socket plates are massive and confluent beneath the umbo forming a large hinge plate which is attached to the roof of the valve medially by a short thick boss. The inner edges of the socket plates are carinate and from the anterior edges of the carinae the spires are derived. No crural plates are developed. The shell material is punctate and the surface bears a dense series of minute depressions which impart a "textile" appearance.

Remarks.—The general form, ornament, punctate shell structure and "textile" sur-

face pattern suggest syringothyrid affinities for this new genus. It differs from *Syringothyris* Winchell in the absence of a transverse plate bearing a syrinx, in the development of costae on the fold and sinus and the much lower cardinal area on the pedicle valve. The same features, apart from the syrinx, separate it also from *Pseudosyrinx*. Weller (1914, p. 404) in his original description of *Pseudosyrinx* noted "Punctate shell structure and fine textile surface markings as in *Syringothyris*." Cooper (1954, p. 332), however, claims that *Pseudosyrinx* is impunctate. Support for this observation is found in specimens from the Lower Carboniferous of New South Wales which are similar in all features to the American species referred by Weller to *Psuedosyrinx*, except that they are definitely impunctate. These forms are being described elsewhere. In the event of *Pseudosyrinx* definitely proving impunctate, then the punctate structure of *Asyrinxia* affords another basis of distinction. The genera *Pseudosyringothyris* Fredericks and *Prosyringothyris* Fredericks both possess a transverse plate and a syrinx-like structure, and should both be relegated to synonymy with *Syringothyris*.

The genera *Syringospira* Kindle and *Sphenospira* Cooper which are costate on the fold and sinus, have much larger pedicle areas, a complex system of delthyrial plates, and in addition impunctate shell structure. From *Spinocyrtia*, some species of which it resembles in form, it differs in its punctate shell structure, costate fold and sinus and its fine surface ornament which is not granulate.

Because of the lack of a transverse delthyrial plate and a syrinx and the absence of a pyramidal pedicle valve it may be suggested that this genus is homeomorphic with the syringothyrids. However the possibility of the appearance of synchronous genera with punctate shell structure, "textile" surface pattern, similarity of general form, simple costation of the lateral slopes and pedicle cardinal areas divided into similar regions of distinct ornament, appears to be too remote to warrant serious consideration. This conclusion is supported by two further considerations. Firstly the division of the cardinal area into regions of vertical and horizontal ornamentation is, so far as I am aware, not known in spiriferoids other than the syringothyrid stock and while the peculiar surface pattern is resembled to some extent by that of certain other genera such as *Spinocyrtia*, it is still definitely distinguishable and apparently unique. In the second place while the costate fold and sinus are features separating *Asyrinxia* from *Syringothyris*, the greater part of the surfaces of both fold and sinus are noncostate, the costae being few and rather rudimentary and restricted to the lateral portions of the fold and sinus.

The relation of this genus to forms usually grouped under *Spirifer distans* Sowerby remains problematical. Some of the forms referred to this species by Davidson have extended hinge lines, relatively low cardinal areas (in comparison with *Syringothyris*), and a feebly plicated fold and sinus all of which suggest *Asyrinxia*, and in addition North (1920, p. 192) states that "There does not appear to be any record of the occurrence of a transverse plate and syrinx in a correctly determined specimen of *S. distans* . . . ". Points of difference however are the tendency to bifurcation of the costae of the lateral slopes, the absence of a threefold division of the cardinal area and the apparent absence of shell punctation (North, 1920, p. 192).

Range.—In New South Wales it is found only in the upper part of the Lower Burindi Group, Upper Tournaisian.

ASYRINXIA LATA (McCoy)
Pl. 16, fig. 1–9

Spirifera lata McCOY, 1847, Ann. Mag. Nat. Hist., vol. 20, p. 233, pl. 13, fig. 7.

Lectotype.—Specimen labelled E 10643 in Sedgwick Museum, Cambridge; from the Tournaisian of Lewinsbrook.

Description of topotypes.—The material in the University of New England from the type locality includes the internal moulds of three brachial valves together with portions of their external moulds and the internal moulds of two pedicle valves together with portions of their counterparts. It is preserved in a blue silty sandstone.

Exterior: The form of the shell is markedly alate the width being approximately four times the length of the valve. The cardinal extremities may be slightly mu-

cronate. The valve appears to have been gently and evenly convex. The commissure between the edge of the sinus and the cardinal extremities is almost straight. The umbo is high and obtuse. The cardinal area is high and is strongly concave. Its surface markings have not been observed. A median sinus is developed from the umbo to the anterior margin. Although its anterolateral portion is poorly plicate, the preservation is not sufficiently good to detect the arrangement of the plicae. The lateral slopes are very gently convex. They bear simple rounded plicae which number approximately 25 on each side of the sinus. The most lateral plicae tend to become insignificant and slightly sinuous, and at the cardinal extremities there appear to be small nonplicate triangular areas. Along the cardinal ridges separating the area from the lateral slopes is a slight smooth ridge on to which the plicae do not extend. The surface of the shell bears a very fine "textile" ornament, and the shell material itself is punctate, the punctae being quite irregularly arranged and having a density of approximately 20 per square mm. on the cardinal extremities, the only position where the shell substance is preserved.

The brachial valve is equally convex with the pedicle valve, and is evenly convex over its whole length. The umbo rises above the general level of the hinge and surmounts a distinct parallel-sided cardinal area which extends the whole width of the valve. The fold is low and well rounded and bears weak plicae on each of its antero-lateral portions. The cardinal margin bears a smooth ridge similar to that of the pedicle valve.

Interior: The pedicle valve is only slightly thickened in the umbo. The dental lamellae are strong, wedge-shaped, subparallel and situated close together. The muscle scars are slightly elevated and rounded anteriorly. Posteriorly the field is divided by three short sharp wedge-shaped ridges, the outer two defining the junction of the adductor and diductor scars, and the central one dividing the adductor scars. These ridges extend half the length of the muscle field.

In the brachial valve the socket plates are long and thickened, and they are confluent below the umbo where they form a short boss-like projection into the valve. The cardinal process is situated immediately beneath the umbo and is supported on the above mentioned boss. The descending lamellae are derived from the inner carinate edges of the socket plates. A very low sharp median ridge divides the adductor scars.

Dimensions (mm.).—

Pedicle valves

Length	Width	Length of muscle field	Width of muscle field	Width of adductor scars
21	78	9	4½	1
24	96			

Brachial valves

Length	Width
22	84 ±
25	90

Remarks.—The above description will be seen to disagree with the original description of McCoy on the following points:

(1) Whereas McCoy states that the cardinal area is flat, in the only specimen available to me which shows the cardinal area, it is strongly concave.

(2) The median sinus is claimed to be smooth. At first sight this appears to be so on the specimens which I have examined but close examination reveals an incipient plication on each side of the sinus. Support is lent to this observation both by the presence of a corresponding plication on the fold of the brachial valve of associated specimens and by the observation of similar plications in the specimens of *A. lata* from Clarencetown described hereunder.

(3) The ribs, according to McCoy, number between sixteen and eighteen on each of the lateral slopes, and "have nearly a third of the length of the sides smooth." On the lateral slope of one of the specimens I have examined there are 25 plicae, the most lateral ones of which are scarcely discernable, and the smooth area is confined to the cardinal extremities. McCoy was working with an internal mould and this was undoubtedly the source of his error.

Associated with similar faunas at Clarencetown, Hilldale and Babbinboon is a species which is similar to the specimens from Lewinsbrook in all essential characters, but which is much larger. There is good reason for believing that the specimens from

Lewinsbrook are either juveniles or forms in which growth has been inhibited by some factor, since they resemble in almost every respect the smaller specimens from the other localities. The only difference is the much smaller separation of the dental lamellae in the specimens from the type locality. The differences may ultimately prove to be of specific rank, but if this be the case they are certainly very closely related. For the present they are all considered under *A. lata* McCoy.

Description of specimens from other localities.—Exterior: The shell is strongly alate even in the largest specimens, but in adults the cardinal extremities become much less acute and the commissure tends to become evenly curved rather than straight.

The cardinal area is high and is pronouncedly concave. Its surface on each side of the delthyrium is divided into two regions in the same manner as *Syringothyris*, the margins of the vertically striated portions diverging from each other at an angle of 120° approximately. The delthyrial angle approximates 40°. The delthyrium has no covering plate but it is always obstructed by a thickening of the shell beneath the umbo, the degree to which obstruction takes place apparently depending on the age of the individual. In one apparently gerontic specimen the delthyrium is completely obstructed for half its length and partly obstructed laterally for the remainder. The margins of the delthyrium are outlined by a narrow groove. The median sinus is broad and well developed. Within it up to six very weak plications may be developed from the bounding plicae, three on each side. These are much narrower and shallower than the proximal plicae of the lateral slopes. In the best preserved specimen these plicae appear to rise at approximately regular intervals of 10 mm. measured from the umbo. Up to 27 plicae have been counted on each of the lateral slopes, the most distal ones being very fine and slightly sinuate. The non-plicate area at the cardinal extremities is almost negligible in size.

The brachial valve is evenly convex. The fold is well rounded at all stages of growth and adults bear three weak plicae laterally.

Interior: In juvenile and adolescent forms the pedicle valve is only slightly thickened posteriorly but in adults thickening becomes pronounced. The dental lamellae in youthful forms are strongly wedge-shaped and well separated, but in gerontic forms they become almost completely enveloped in the thickened shell. The muscle field is relatively broad and is divided by the three ridges as described in the topotypes. The shoulders are deeply scarred by elongate ovarian pits.

In the brachial valve the socket plates are greatly thickened and unite beneath the umbo to form a short thick plate about 2–4 mm. long in adult specimens. Their inner edges become carinate and give rise to the descending lamellae. The spires are very elongate. They have not been observed in an undisturbed state and no details concerning their direction, number of volutions or the jugum are available. However one specimen in which 22 volutions are *visible* has been found. The adductor scars are elongate and elliptical in outline and are situated in the middle of the valve, well forward from the umbo. In adults the median ridge arises 2 or 3 mm. anterior to the end of the junction of the socket plates and extends slightly beyond the anterior extremity of the adductor scars. It is usually a well-rounded structure but may bear a faint median groove between the adductor scars.

Remarks.—Minato (1951, p. 373; 1952, p. 160) has described and figured a spiriferoid species from the Jumonji Stage of the Kitakami Mountains as *Fusella nipponotrigonalis*. His interpretation of *Fusella* is based upon Buckman's diagnosis (1908, p. 29) which is very broad and embodies his (Buckman's) views upon the categenetic development of certain groups of spiriferids. The relationship between *Fusella nipponotrigonalis* Minato and the genotype *Spirifer fusiformis* Phillips is very remote. The former species resembles *Asyrinxia* in general form, the moderately high cardinal area, the simple lateral plications, the presence of strong dental lamellae (see Minato, 1952, pl. 11, fig. 3), the deep division within the umbo of the brachial valve, and the rounded median ridge (see p. 192, pl. 6, fig. 6). No mention is made in the description of shell punctation, though this may be due to a lack of shelly material, since all of the published figures are of moulds. Also the

surface is said to be concentrically striate, no mention is made of the "textile" surface pattern of *Asyrinxia*, and the fold is said to be non-plicate except for weak sulci at the umbonal region. Once again these apparent differences may be due to deficiencies in the extremely poor Japanese material. It is interesting to note that McCoy's original description of *Asyrinxia lata* was lacking on the same points.

If *Fusella nipponotrigonalis* is as I have outlined above, then it is the only species of *Asyrinxia* yet recognised outside of New South Wales. It is found in the Jumonji and Maide? Stages, which are of Upper Tournaisian and Lower Viséan age respectively.

Range.—As for the genus.

Family RHYNCHOSPIRINIDAE Schuchert & Levene, 1929

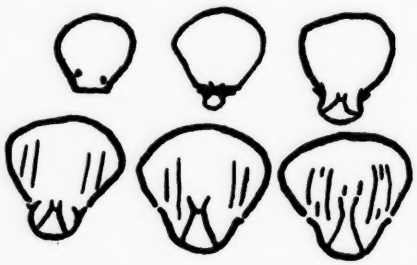
Genus EUMETRIA Hall

Genotype: *Retzia vera* Hall.

Diagnosis.—Included in this genus are small to medium sized, subequally biconvex, rostrate shells with a short straight hinge line and costate to costellate ornamentation. The umbo is truncated by a large circular foramen, which is lined by a small pedicle collar. The delthyrium meets the foramen only at its apex. The cardinal area is restricted to a small flattened extension on either side of the delthyrium. The cardinal extremities of the brachial valve are produced into small flattened auriculations. The shell material is densely punctate. The pedicle valve is without dental lamellae. The hinge plate of the brachial valve bears two curved projections of variable length which extend into the umbo of the pedicle valve and lie close to the deltidium. The hinge plate itself is quite short, and is supported on two long slender almost vertical plates which arise in the umbo and are up to half as long as the valve. These plates may or may not be united by a spondylioid process which is an anterior extension from the hinge plate. They increase in height anteriorly and from their antero-ventral edges the descending lamellae of the brachia are derived. The spires, with up to nine volutions, are directed laterally.

Remarks.—Dr. G. A. Cooper of the United States National Museum has generously provided me with some specimens of the genotype of *Eumetria*, *E. vera* Hall, from the Chester Series and with an excellent set of photographs of the holotype of *Acambona prima* White. The serial sections of a small specimen of *E. vera* are reproduced in Text-fig. 23.

It is important to note the general agreement between *E. vera* and *E.? mona*, n. sp., in internal structure: there are no dental lamellae; the brachial hinge plate is short; two discrete plates project posteriorly from the hinge plate into the umbo of the pedicle valve; two high septum-like plates which increase rapidly in height anterior to the articulation, give rise to the descending lamellae. The major difference is the presence of a connecting plate between the two vertical supporting plates in the brachial valve of *E. vera* giving the appearance of a "long narrow concave or spoon shaped central process with sharply elevated edges." This plate is apparently present in all of the American species of *Eumetria*, and therefore its absence in *E.? mona*, n. sp., suggests that this species is probably generically distinct. Externally *E.? mona* closely resembles *Acambona prima* White. Unfortunately the internal structures of the brachial valve of that species remain unknown and significant comparisons are therefore impossible. Should this species prove to lack the connecting plate found in



TEXT-FIG. *23*—Serial sections through the umbo of a specimen of *Eumetria vera* Hall from the Chester Series of Illinois. ×2. The sections have been cut at intervals of approximately 0.3 mm. Due to the state of preservation difficulty was experienced in the interpretation of the second section, where it was almost impossible to distinguish the structures of the two valves. The figure illustrates what is considered to be the most probable condition.

Eumetria there would be no doubt that such a plate is of generic significance, and that *E.? mona* should be placed in the genus *Acambona*. However, until the structure of *A. prima* has been elucidated, I prefer to place the species herein described tentatively into *Eumetria*.

Range.—In America *Eumetria* ranges through the Mississippian. *Acambona* however appears to be restricted to the Burlington limestone of Upper Tournaisian age. Forms with affinities to *Eumetria* have been found in the Tournaisian of Britain (Davidson, 1862), Belgium (de Koninck, 1843), the Moscow Basin (Sarycheva & Sokolskaya, 1952), the Kuznetsk Basin (Tolmachoff, 1926) and Australia (Etheridge, 1892).

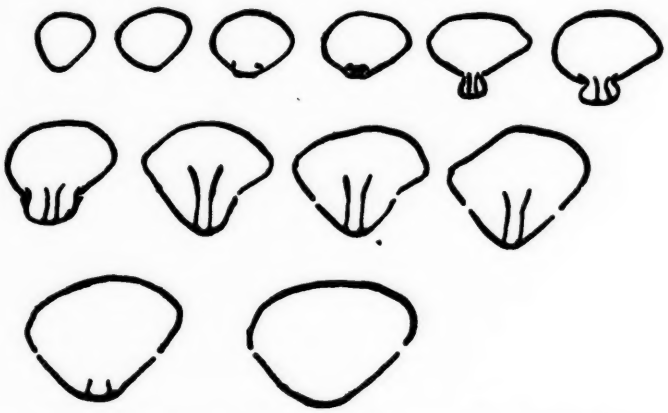
EUMETRIA? MONA, n. sp.
Pl. 15, fig. 8,9

Holotype.—F. 2812. University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The pedicle valve is strongly convex with its greatest convexity posteriorly. In anterior view the valve is evenly convex. In outline the valve is elongate, being two-thirds as wide as long. The greatest width is at approximately two-thirds the length of the valve. The umbo is very high and strongly curved. The cardinal area is not clearly defined on any of the available specimens but this may be due to poor preservation. The tip of the umbo is occupied by a large rounded pedicle foramen, 2.5 mm. in diameter in adults. The delthyrium is large and triangular and meets the foramen only at its apex. It is completely covered, but the nature of the covering plates is uncertain. Since no median suture is visible, I am inclined to think that they are fused deltidial plates, though because the material is rather poor this should be regarded as tentative only. The umbonal slopes are rather angular and reach the margin of the valve at the mid-length position. Ornament consists of simple rounded costae which are continuous from the umbo to the anterior margin. There are 45–50 costae between the umbonal ridges, the size of the costae decreasing laterally. Between the umbonal ridges and the margins of the delthyrium the costae are weak to absent, and their number cannot be accurately determined from the present specimens.

The brachial valve is markedly triangular posteriorly and is rounded anteriorly. In anterior profile the valve is evenly convex. The valve is slightly more convex toward the umbo than the anterior. The umbo is sharp and is tucked in beneath the delthyrium. The hinge line is short (approx. 8 mm.), and at its extremities it is compressed to form minute ears. Its surface is ornamented with 55–60 costae of the same type as those of the pedicle valve.

Interior: The pedicle valve is devoid of dental lamellae. Even though the internal surface has been well prepared no muscle scars are visible. Most of the interior surface is costate.



TEXT-FIG. *24*—Serial sections through the umbo of a specimen of *Eumetria? mona*, n. sp. ×1.

The brachial valve has two very long deep plates reaching from the umbo almost one-third of the distance to the anterior margin. Their posterior edges are produced into dorsally concave processes which project into the umbo of the pedicle valve. Over most of their length the ventral edges of the plates are slightly splayed. Just anterior to the articulation the height of the plates rapidly increases, and they project well into the pedicle valve. From this point they are gradually reduced in height and sharply truncated at their anterior margin. The descending lamellae and the brachidium are unknown.

Remarks.—*Acambona prima* is very similar in size, form and ornament to *E.? mona*, n. sp. The pedicle valve of the species is without dental lamellae but as yet no description of the vital internal structures of the brachial valve has been forthcoming, and thus detailed comparisons are not possible. It is not similar to any other American species of *Eumetria*.

De Koninck (1843) described the species *Acambona serpentina* de Koninck from the Tournaisian of Belgium, and later considered that it is probably identical with *Acambona prima* White. Unfortunately de Koninck did not describe the internal structures of his species and so far as I am aware no description has been forthcoming subsequently. From the description and figures the Belgian species appears to be closely comparable externally with *E.? mona*. It is interesting to note that Tolmachoff (1926) has found similar material in the Tournaisian of the Kuznetsk basin and Nalivkin (1937) has described forms which he relates to *Acambona prima* from the Upper Tournaisian and Lower Viséan of Kazakhstan.

I have re-examined the specimen from the Lower Carboniferous of the Rockhampton District of central Queensland, referred by Etheridge (1892, p. 242, pl. 11, fig. 20–22) to *Retzia? lilymerensis* Etheridge. Externally there is nothing to suggest that this species is not a *Eumetria*. However the internal structure is not shown, and since no further material is available for sectioning it is impossible to give a precise determination.

Range.—This species is known only from the type locality, Upper Tournaisian.

Superfamily TEREBRATULACEA Waagen, 1883

Family DIELASMATIDAE Schuchert, 1913

Genus BALANOCONCHA, n. gen.

Genotype: *Balanoconcha elliptica*, n. sp.

Diagnosis.—The shell is of medium size and is terebratuliform in outline. The surface is smooth except for a few irregular growth lamellae. The commissure is either rectimarginate or very slightly sinuate. Deltidial plates are small and conjunct. Muscle scars of both valves are inconspicuous. No dental lamellae are developed. The cardinal process is small and the cardinal plate consists of a central crural trough which is attached only to the roof of the valve anteriorly but posteriorly it is also attached by crural plates to the socket plates. The shell material is densely punctate, the punctae being arranged irregularly, though occasional small areas may show an almost regular linear arrangement. Approximately 400–450 punctae occur per square mm. on the central portion of the valves.

Remarks.—This genus can be readily distinguished from *Dielasma* King by the absence of dental lamellae. So far as I am aware the brachial internal structure of the genotype of *Dielasma*, *Terebratula elongata* Schlotheim, has not been adequately studied and no comparison can be made.[1] It differs from *Dielasma* as interpreted by Weller in the absence of dental lamellae and in development of the distinctive crural trough.

The brachial internal structure seems to be closest to *Dielasmoides* Weller, which also has a sessile cardinal plate, but differs in not having a crural trough, and in having well developed dental lamellae.

The external form is not distinctive.

Range.—This is the only locality at which it has been found up till the present.

BALANOCONCHA ELLIPTICA, n. sp.

Pl. 15, fig. 13–15; Text-fig. 25–27

Dielasma sacculum (Martin) var. *hastata* (Sowerby), DUN & BENSON, 1920, Proc. Linn. Soc. New South Wales, vol. 45, no. 179, p. 346, pl. 19, fig. 12.

[1] Since this paper went to press Stehli (1956, Jour. Paleont., vol. 30, p. 299) has published on topotypes of *T. elongata*. His work confirms the distinctness of *Dielasma* and *Balanoconcha*.

Diclasma sacculum (Martin) var. *amygdala* (Dana), DUN & BENSON, 1920, Proc. Linn. Soc. New South Wales, vol. 45, no. 179, p. 347, text-fig. 12.

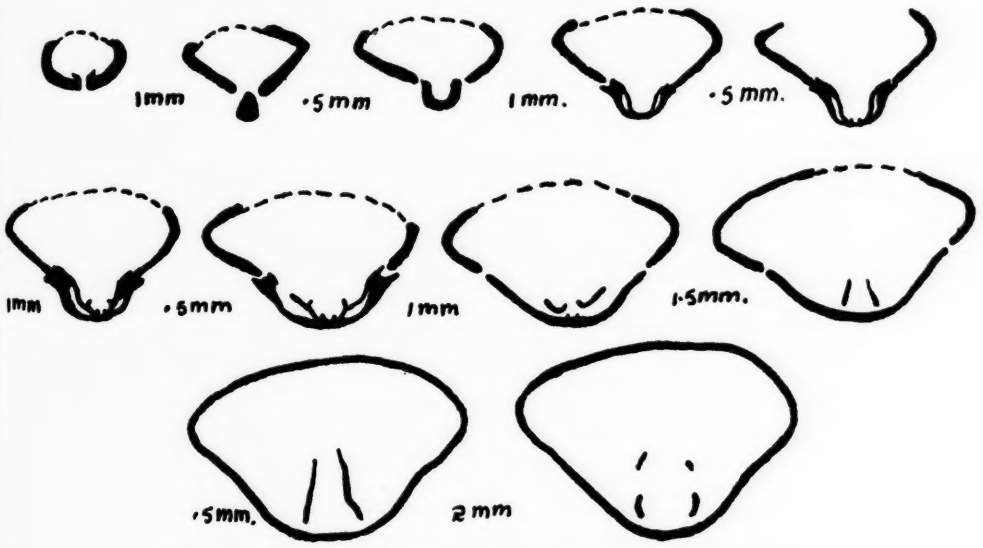
Holotype.—F. 2825 University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The shell is of medium size and is terebratuliform in outline. The pedicle umbo is suberect and the foramen is mesothyrid to permesothyrid. The deltidial plates are small and conjunct and in certain specimens appear to be fused. A well developed pedicle collar occurs in all specimens. The beak ridges are subangular separating off narrow slightly concave palintropes which are approximately one third of the total length of the valve. The cardinal margin is terebratulid. The anterior and antero-lateral margins are evenly rounded but the posterolateral margins are almost straight imparting a broad wedge-shape to the umbo. The commissure is rectimarginate. The surface is smooth except for irregularly developed growth lines. The shell material is densely punctate, there being 400–450 punctae per square mm. The punctae are in general irregularly distributed though small random areas may exhibit an almost regular linear arrangement.

The brachial valve is slightly less convex than the pedicle. It is similar in outline but the umbo is much more obtuse.

Interior: No dental lamellae are developed. The teeth are slightly thickened. In adults a broad low rounded median ridge arises at a variable distance (2 to 6 mm.) from the umbo and extends approximately four-fifths of the total length of the valve. Lateral to this in well preserved specimens are two or three poorly defined slightly diverging pallial trunks, two of which are more prominent than the others. The muscle scars are not defined.

The cardinal process is small and is in the form of an open inverted V. The cardinal plate is complex. It consists of a centrally situated crural trough whose anterior ends are free and extend forward on the roof of the valve a distance of approximately 10 mm. from the umbo in adults, but whose posterior portion is firmly attached to the inner margins of the socket plates by means of stout crural plates. The crurae arise from the junction between the crural trough and the lateral crural plates. Originally they are concave ventrally but rapidly flatten out



TEXT-FIG. *25*—Serial sections through the umbo of *B. elliptica* n. sp. ×2.

TEXT-FIG. *26*—Enlarged diagrammatic sections through the umbo of the brachial valve of *B. elliptica*, n. sp. These sketches have been taken from specimens cut at different positions. ×1.5.

and bear long crural points. The form of the loop remains unknown. A large pallial sinus borders the crural trough on each side. These broaden and unite just anterior to the crural trough and then diverge slightly antero-laterally, making an angle of 20°–25° with each other. They become progressively narrower and less well defined and are usually indistinguishable within 5 mm. of the anterior margin. Along its axis the crural trough may bear one or two very faint ridges which are apparently associated with the adductor scars which are borne in the trough.

Remarks.—It has been customary in Australia to refer all Upper Paleozoic Terebratulacea to the genus *Dielasma*. Dun & Benson (1920) referred this species to Martin's *Dielasma sacculum* and divided it into two varieties *D. s.* var. *hastata* (Sowerby) which is from the Carboniferous limestone of England and *D. s.* var. *amygdala* (Dana) which is probably from the Permian of the south coast of New South Wales. They made no examination of the internal structure of the shells, but made their divisions on external form, *D. amygdala* Dana differing from *D. hastata* Sowerby "in its very elongate form." This is a notoriously unreliable basis for taxonomic distinction. Even so, on the basis of their figures and measurements it is difficult to see any real difference. For example the length, breadth and thickness of the specimen referred to *D. amygdala* (Dana) are 27 mm., 17 mm., and 12 mm., respectively, and the corresponding measurements for one of the *D. hastata* specimens are 27 mm., 16 mm. and indeterminate.

Most of the specimens from this locality are significantly distorted, but an examination of a large collection has indicated that the population is completely homogeneous.

Range.—As for the genus.

Superfamily RHYNCHONELLACEA Schuchert, 1896

Family CAMAROTOECHIIDAE Schuchert & Levene, 1929

Subfamily CAMAROTOECHIINAE Schuchert & Levene, 1929

Genus TETRACAMERA Weller, 1910

Genotype: *Rhynchonella subcuneata* Hall.

Diagnosis.—Rhynchonelliform shells in the pedicle valve of which is a large spondylium braced to the lateral walls of the valve by two strong plates. The brachial valve has a divided hinge plate which is supported on a strong median septum. The structures lateral to the median septum are variable. The margins of both valves are flexed almost at right angles to the plane of junction of the valves.

Remarks.—The course adopted by Weller in interpreting this genus I consider to be sound, though I have not had the opportunity of examining any of the American species. The peculiar arrangement of the internal plates in the pedicle valve is itself a strong indication of the homogeneity of the group; but since this is invariably coupled with a divided hinge plate in the brachial valve and flexed margins in both valves, the matter is beyond dispute. The wide range of variation in the brachial internal plates is of specific significance only. This is of particular interest since in most other Palaeozoic members of the Rhynchonellacea the internal structures of the brachial valves are relatively constant and are of generic value. Analogous phenomena have been found in the Spiriferacea, e.g., in most genera in this group the internal structures are constant, but in *Phricodothyris* there is a wide range of variation in the development of the median septum of the pedicle valve and in certain Rostrospiracea such as *Crurithyris* the internal plates of the brachial valve are unusually variable (George, 1932, p. 533; 1931, p. 39).

Range.—So far as I am aware, *Tetracamera* has been recorded up till the present only from the Lower Mississippian of North America. According to Weller et al. (1948,

p. 114) the *Tetracamera* zone "overlaps the boundary between the Meramecian and Osagean series and embraces beds ranging from Keokuk to Salem."

TETRACAMERA cf. T. SUBTRIGONA (Meek & Worthen)
Pl. 15, fig. 10,11; Text-fig. 27

Material.—F. 2710–11 University of New England Collections.

Description.—Exterior: Only two specimens have been located. One crushed specimen has both valves present, and the other is a perfectly preserved pedicle valve. The pedicle valve is slightly convex and subtrigonal in outline. The umbo is high and pointed. The margins of the shell are abruptly deflected and lie almost at right angles to the plane of the valve. The plications are stong and subangular, five of them being in the sinus, five on each of the lateral slopes, and four or five on each of the postero-lateral deflections. These latter do not reach to the umbo. The sinus is shallow but is produced into a high tongue anteriorly.

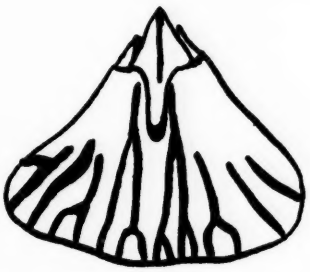
The brachial valve appears to have been much more convex than the pedicle valve, although crushing has flattened it. Its margins are deflected in the same way as those of the pedicle valve. There are six strong plicae on the fold and four or five on each of the lateral slopes.

Interior: The pedicle valve bears a very strong spondylium in its posterior portion, extending one half the length of the valve. Anteriorly the plates gradually decrease in height but the structure is continued forward on the floor of the valve by a short thick ridge. Laterally the sides of the spondylium are supported to the walls of the valve by means of two strong plates.

The pallial sinuses are well developed and their arrangement is illustrated in Text-fig. 27.

The brachial valve has a high narrow median septum which extends approximately one quarter of the distance to the flexed region. Posteriorly it divides to form a spondylioid hinge plate. Lateral to the hinge plate are two long cavities which are split along their ventral surfaces. Further details could not be observed.

Remarks.—This form has the typical tetracamerid internal structure of the pedicle valve and the deflected valve margins typical of all species of *Tetracamera*. The internal structure of the brachial valve appears to be close to that of *T. subtrigona* (Meek & Worthen), though it may be slightly more complex. It is impossible to make an accurate comparison because of the poverty of the material available. In general form and in the number and arrangement of the plicae it is very similar to *T. subtrigona*. The chief points of difference are the longer median septa in both the pedicle and brachial valves, and the relatively broader outline and slightly less complex structure in the interior of the brachial valve of the American form. It is worthy of note that this latter feature is very variable in all of the species described by Weller (1914).



TEXT-FIG. *27*—Diagrammatic illustration of the pallial sinuses of the pedicle valve of *T.* cf. *T. subtrigona*. ×1.6.

The present form is thus probably specifically distinct from *T. subtrigona* but there is insufficient material available for the erection of a new species. *T. subtrigona* in America is found only in the Keokuk limestone which is correlated with the uppermost Tournaisian of Europe.

Range.—Up till the present this species is known only from this locality, Upper Tournaisian.

Genus PUGNAX Hall & Clarke
Genotype: *Terebratula acuminata* J. Sowerby, 1822

Description.—Rhynchonelliform shells variable in size, which have a marked linguiform extension of variable shape at the anterior margins. Both valves may be either smooth or have smooth umbonal regions with vari-

able plicae anteriorly. In the interior of the pedicle valve dental lamellae of variable strength are developed. The hinge plate of the brachial valve is divided and is unsupported by a median septum, but a low median ridge may be present.

Remarks.—The International Commission on Zoological Nomenclature in 1948 held the name *Conchyliolithus Anomites acuminatus* Martin to be invalid. Muir-Wood (1951) has pointed out that the specific name *acuminatus* was next used in the same sense by Sowerby 1822, in the combination *Terebratula acuminata*, and that Sowerby's species therefore becomes the genotype of *Pugnax*. A lectotype is figured by Muir-Wood (1951, plate 111, fig. 1a,b and c).

The genotype has been further discussed by Parkinson (1954) who states that the internal structure of the species is essentially the same as Weller (1914) had indicated for *P. pugnus*.

Range.—In Europe and America *Pugnax* comes in at the base of the Middle Devonian and ranges through to the end of the Dinantian.

PUGNAX MINUTUS, n. sp.
Pl. 15, fig. 16–18

Holotype.—F. 2819. University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—Exterior: The pedicle valve is slightly wider than long. It is only slightly convex the greatest convexity being across the posterior third of the valve. The posterolateral margins are straight but the anterolateral margins are gently curved. The umbo is moderately high and pointed. The false cardinal areas are well developed. The median sinus originates between one-quarter and one-half of the distance from the umbo to the anterior margin. It rapidly deepens and is produced into a high tongue anteriorly. The plicae originate at the same stage as the sinus, the umbonal shoulders being smooth. There are two to four plicae in the sinus and from three to six on each of the lateral slopes.

The brachial valve is much more strongly convex than the pedicle valve. The highest point is at or near the anterior margin, the curvature being rather slight along the anterior part of the fold but much stronger toward the umbo. The lateral slopes are convex and steep. The fold bears three to five, and each of the lateral slopes from three to five plicae, all of which originate at a distance of one third of the length of the valve from the umbo.

Interior: The pedicle valve has two short dental lamellae. The brachial valve has a divided hinge plate unsupported by a median septum, but a low rounded ridge runs for a distance of 1–1½ mm. anterior from the umbo.

Remarks.—The American species *Pugnax wortheni* (Hall) from the Salem limestone (Lower Viséan) of Illinois is similar to *P. minutus*, n. sp., in size and form but it has fewer plicae on the lateral slopes and in the sinus.

Range.—This species is so far known only from the type locality—Upper Tournaisian.

Genus CAMAROTOECHIA Hall & Clarke
Genotype: *Atrypa congregata* Conrad.

Remarks. The structure of this genus is well established and there is nothing to add to the accounts given by Weller (1914, p. 175), Tien (1938, p. 29 et seq.), and Maxwell (1954, p. 13).

Range.—In both Europe and America *Camarotoechia* appears to range from the Silurian to the end of the Dinantian (Mailleux, 1935; Cooper, 1944). In Australia it has been recorded in beds of Silurian age by Shearsby (1911), Upper Devonian and Tournaisian age by Maxwell (1954) and from rocks of supposedly Permian age in Western Australia by Prendergast (1935). It is possible that these beds may prove to be younger. Shearsby's material has never been critically re-examined.

CAMAROTOECHIA sp.
Pl. 15, fig. 12

Description.—Exterior: The pedicle valve is slightly convex and is subtrigonal in outline. The umbo is small. The median sinus is present only on the anterior third of the valve but it develops rapidly into a high tongue. There are eighteen subrounded plicae present, four of which are situated in the sinus.

The brachial valve is much more convex than the pedicle valve, its highest point be-

ing at the anterior edge of the fold. The median fold originates near the middle of the valve and is high anteriorly. The umbo is small and tucked beneath the pedicle umbo. The lateral slopes bear plicae of the same type as those of the pedicle valve. On the fold there are five plicae, the three central ones being larger and more angular than the two laterals.

Interior: The pedicle valve has long fine dental lamellae. The hinge plate of the pedicle valve is thickened and is supported on a very fine median septum. The crural cavity is very short. In the only specimen available the crural cavity appears to be carried forward for a distance of approximately 0.2 mm. as a spondylioid structure on the median septum. The crura have three-rayed arrangement posteriorly.

Dimensions (mm.).—

Length	Width	Height	Height of fold
11	14	8½	6±

Remarks.—Only two specimens of this species have been found. The internal structure of the brachial valve appears to be distinctive. The external forms of most of the species of this genus are extremely variable so that comparisons based only on a study of the exterior are almost certainly spurious. The internal structures of most species have not been illustrated.

Phylum COELENTERATA
Class ANTHOZOA
Sub Class ZOANTHARIA
Order RUGOSA
Family CANINIIDAE
Genus CANINOPHYLLUM Lewis, 1929
Genotype: *Cyathophyllum archiaci* Milne-Edwards & Haime.

Diagnosis.—These are median to large solitary trochoid corals, in which the major septa are long and meet at the axis to form a loose irregular and sometimes impersistent axial structure. The counter septum is elongate in the juvenile stage. The cardinal septum is reduced in the adolescent and adult stages. Dilatation of the major septa in the tabularium occurs throughout growth, the septa of the cardinal quadrants being more strongly dilated than those of the counter quadrants. The fossula is closed except in the adult stages. The dissepimentarium in adults is broad and the dissepiments are fine. The tabulae are fine, incomplete and irregular.

Remarks.—The relationship between *Bothrophyllum* Stuckenberg and *Caninophyllum* Lewis is obscure. Lewis (1929) in his discussion of his new genus made no reference to *Bothrophyllum*, his only comparisons being made with *Caninia*. The distinguishing features of *Caninophyllum* according to Lewis are the broad dissepimentarium with a fine mesh of angulo-concentric dissepiments and the absence of a breviseptal phase. In the holotype of *C. archiaci* (Milne-Edwards & Haime) the major septa are not strongly thickened in either the early neanic or ephebic stages, though those in the cardinal quadrants are thickened in the late neanic stage. At all stages a loose axial structure of septal origin is present though not all of the major septa are involved (Lewis, 1929, pl. 11, fig. 1a–c). In other specimens referred to the same species by Lewis (e.g. pl. 11, fig. 2a–g) the axial structure is weak or absent, and the septa are dilated at all stages of growth.

Bothrophyllum conicum (Trautschold) exhibits a similar range of variation. The forms referred by Dobrolyubova (1940, pl. 6, fig. 8–14) to *B. conicum* var. *robusta* show no axial structure, and those referred to *B. conicum* itself (pl. 4) show very weak axial developments, while most specimens of the species have the structure well developed. There is also marked variation in the degree of dilatation of the septa (compare Dobrolyubova, pl. 4, fig. 2–6 with pl. 6, fig. 2–6). Moreover, the dissepiments in *B. conicum* can be markedly angular (ibid., pl. 4; pl. 5) and seem to differ in no way from those of *Caninophyllum*.

Hill (1956) states that one point of difference between the two genera is the presence in *Bothrophyllum* of an elongate counter septum which joins with the ends of the major septa to form the axial structure. It is worthy of note in this connection that in some specimens of *C. archiaci* an elongate counter septum appears at certain growth stages (e.g., Lewis, 1929, pl. 12, fig. 1e,3). Further, the tabulae of *C. archiaci* tend to be complete while those of *B. conicum* are usually incomplete; and the cardinal fossula

of the former is inclined to broaden towards its axial end to produce a weakly club-shaped structure, a feature rarely exhibited by the latter.

It may well be that the differences between *C. archiaci* and *B. conicum* are of specific rather than generic value, and the two genera may be found to merge.

Range.—The genotype of *Caninophyllum* is from the Upper Viséan of North Wales, but the genus itself ranges from the Upper Tournaisian to the Upper Viséan in western Europe. In Russia it has been recorded in beds ranging from the Tournaisian C_1^1 to the Upper Carboniferous C_3^3. *Bothrophyllum* in Russia has a more restricted range, from the Moscovian C_2^1 to the *Triticites* beds C_3^3. In Western Europe, *Bothrophyllum* (usually under the designation of the synonym *Pseudocaninia*) occurs only in the Viséan. Neither *Bothrophyllum* nor *Caninophyllum* is known to occur in southern or eastern Asia, North or South America or Africa.

Caninophyllum sumphuens (Etheridge)
Pl. 17, fig. 1–5

Zaphrentis? sumphuens Etheridge, 1891, Mon. Geol. Survey New South Wales, Paleont. 5, p. 16, pl. 11, fig. 4–6.

Holotype.—Originally F. 1458 Geol. Survey New South Wales Collection; now F. 46215 Australian Museum Collection.

Description.—The corallum is simple, robust and trochoid. The largest specimen has a maximum diameter of approximately 45 mm. near the top of the calyx and its total estimated length is in the vicinity of 90 mm. Another nearly complete specimen has a maximum diameter of 45 mm. and a total length of 75 mm. All of the specimens have been considerably washed about, and the epitheca, and in many cases the dissepimentarium, have been removed. The form of the calyx is unknown although it is known to be very deep.

At the base of the calyx in the largest specimen there are 59 major septa and a similar number of minor septa. In the adult stage the major septa are flexed and may end freely or be confluent in irregular groups at their axial ends forming a very loose irregular axial structure. In the tabularium they are strongly dilated in a lanceolate fashion, but they are not in contact with their neighbors except at the outer margin of the tabularium. However they may not be in contact around the whole corallite. The cardinal septum and the major septum on either side of it are dilated in the dissepimentarium as well as in the tabularium. The cardinal septum is short, extending between one-third and one-quarter of the distance to the axis. The major septa are usually continuous within the dissepimentarium, but may rarely be discontinuous. The minor septa however are characteristically discontinuous in the dissepimentarium. Occasionally the thickened tips of the minor septa may extend into the tabularium.

In the calyx the major septa all become much less dilated though those in the cardinal quadrants remain dilated at a later stage than do those in the counter quadrants.

The cardinal fossula is narrow and more or less parallel sided. It is most commonly open, though it may be partially closed by the irregular flexing of the free ends of the septa in the cardinal portions of the cardinal quadrants. CL 11^1 bounds the fossula over four-fifths or more of its length and CL 10, CL 9 and CL 8 are progressively longer. CL 7 is a normal sized septum. Septal insertion is accelerated in the counter quadrants, the adult pattern being seventeen major septa in each of the counter quadrants and eleven in each of the alars. The counter septum may be either longer or shorter than those on either side of it.

Due to abrasion prior to burial the dissepimentarium is largely removed from most corallites. In the best preserved specimen, the width of the dissepimentarium at the base of the calyx is approximately one-quarter of the radius of the corallite. The dissepiments are closely spaced and are very fine. In vertical section they are seen to be almost vertically inclined.

The tabulae are very tenuous and incomplete, the strongly dilated septa tending to crowd them out. They are almost invariably turned down around the margin of the tabularium. Axially they are very variable ranging from highly arched to gently sagging.

[1] The septal notation here used is that of R. G. S. Hudson, 1936, Yorkshire Geol. Assoc., Proc., vol. 23, p. 68.

Ontogeny.—The earliest stage examined was at a corallite diameter of 7 mm. where there were 30 major septa, six of which are in each of the alar quadrants and eight in each of the counter lateral quadrants. The septa in all quadrants are in fascicles which are confluent axially. The cardinal septum reaches to the axis and its axial end may be strongly dilated. The counter septum also reaches to the axis but cardinal and counter septa do not always meet end to end. All of the septa are dilated, but they are not laterally contiguous except at the periphery of the corallite. This general pattern is maintained until the corallite has a diameter of from 10–12 mm. and a septal count of 30–35.

Beyond this stage the cardinal and counter septa tend to be reduced in length and some of the other septa tend to end more freely. The strength of the axial septal complex is reduced in some specimens. The thickened ends of minor septa occasionally appear, but no dissepiments have been observed, perhaps because of the poor preservation. At a diameter of 14–15 mm. there are approximately 38 septa present, eight in each of the alar quadrants and ten in each of the counter laterals. In one specimen of diameter approximately 15 mm. there is a narrow marginal zone in which undilated major and minor septa occur, but no dissepiments are found in it.

In some specimens the septa withdraw from the axis at a corallite diameter between about 15 and 20 mm. but the loose axial septal structure is reformed at later stages in the ontogeny.

At a diameter of 20–22 mm. there are 40–45 septa established on the adult pattern. A common arrangement is nine septa in each of the cardinal and twelve in each of the counter quadrants. The dissepimentarsium is well etablished.

At diameters circa 30 mm. arrangements of Cl, CL 10, KL 14 or 15, Kl are common, while at 35 mm. Cl, CL 10 or 11, KL 16, Kl, dominate. In the largest specimen (diameter 45 mm.) the arrangement is Cl, CL 11, KL 17, Kl. Thus from a diameter of 7 mm. (the neanic stage) onwards the relative rates of insertion of the septa in the cardinal and counter quadrants remain constant.

Remarks.—There is considerable resemblance between this species and the "*monense*" variety of the genotype *C. archiaci* (Milne-Edwards & Haime) described by Lewis from the S_2–D_1 beds of Britain. The chief differences are the more regular and more closely spaced tabulae, and the broader dissepimentarium in the European species.

I have examined the holotype of *C. sumphuens*, and after a study of its structure and preservation and the sediment in which it is preserved, I am convinced that it was collected from Watts, Babbinboon, which is only six miles to the south-west of Somerton, the locality named by Etheridge.

Range.—At present this species is known only from the Upper Tournaisian of Watts, Babbinboon. Etheridge (1891, p. 17) states that the horizon is doubtful but is in the "Upper Marine Series," which is now known to be of Permian age. There are no beds belonging to the Upper Marine Series in the neighborhood of Somerton.

Family LITHOSTROTIONTIDAE
Genus LITHOSTROTION Fleming, 1828
Genotype: *Lithostrotion striatum* Fleming, 1828

Remarks.—This genus has been adequately discussed by Hill (1940).

LITHOSTROTION COLUMNARE Etheridge

Lithostrotion? columnare ETHERIDGE, 1900, Geol. Survey Queensland, Bull. 12, p. 18, pl. 1, fig. 1; pl. 2, fig. 1–5.
Lithostrotion columnare Etheridge. HILL, 1934, Royal Soc. Queensland, Proc., vol. 45, no. 12, p. 84, pl. 10, fig. 18–25.

Material.—F. 2895–96 University of New England Collections.

Remarks.—Two boulders of solid coralline limestone with maximum diameters of 13 and 20 cm. have been found at this locality. Since frequent visits to this area are made by students who also visit the nearby Viséan *Lithostrotion* limestone in the Lower Kuttung Group, the possibility that these two boulders had been dropped by a previous collecting party has been suggested. This, however, would not appear to be probable since both of these specimens were collected from the southeastern side of the outcrop which is seldom visited by collecting parties, and in addition, when found, both specimens were deeply embedded in the usual sandy

matrix of the locality. They probably were derived from some nearby reef-like deposit which at present remains unlocated.

The average corallite diameter is 7–8 mm. The septa are rather thin, and there are eighteen to twenty of each order, rather less than the usual number in *L. columnare* Etheridge which according to Hill (1934) is 20–25. However specimens with a smaller number of septa and a smaller average corallite diameter than normal are included within the species (e.g., Hill, 1934, pl. 10, fig. 21,22).

The corallite walls vary greatly in thickness and may be so reduced as to approach astracoid structure. Both normal and lonsdaleoid dissepimentaria have been observed. The tabulae are tent shaped off the styliform columella, and there is no clear differentiation into an inner and outer series of plates.

Range.—Upper Tournaisian to Upper Viséan. This discovery is of particular interest since the species was known previously only from the Upper Viséan. The comparison of specimens from the marine intercalation in the Lower Kuttung rocks at Babbinboon (Carey, 1937, p. 351), some 3000 ft. above the Watts locality (where they are associated with an *Amygdalophyllum—Aphrophyllum* fauna) has shown that these differ in no way from the specimens described here.

Overseas, species of this type are not known to occur below the base of the Viséan.

LITHOSTROTION VOISEYI, n. sp.
Pl. 17, fig. 6–8

Holotype.—F. 2892, University of New England Collections; from the Upper Tournaisian of Watts, Babbinboon.

Description.—The corallum is dendroid to subphaceloid in form. The corallites are very variable in size, the largest observed being 17 mm. in diameter. Only lateral increase has been observed.

There are 26–33 septa of each order in adult corallites, all of them being slightly thickened in the tabularium. The major septa are typically straight and confluent with the columella though diphymorph individuals are occasionally present. The minor septa are comparatively long, usually about one quarter of the corallite diameter in length. The columella is robust, rounded or elliptical in outline, and in many corallites it is continuous with the counter septum which is thickened towards its axial end. The tabellae are divided into two series: an inner steeply inclined set in which the plates are almost straight or convex upwards and outwards, and an outer flatter-lying set in which the plates tend to be concave upwards. The dissepimentarium is slightly less than half the width of the corallite and is composed of from three to six series of small steeply inclined plates. A tendency towards lonsdaleoid structure occurs in some corallites.

Remarks.—This new species is related to *L. stanvellense* Etheridge, a broadly interpreted species which in the past has been considered to typify the Viséan D_2 limestones of Queensland and Northern New South Wales. The types of *L. stanvellense* (as figured by Etheridge, 1900, and Smith, 1920), differ from *L. voiseyi* in their unthickened septa, the lack of continuity between an axially thickened counter septum and the columella, the shorter minor septa and the narrower dissepimentarium with only two or three series of plates.

Populations of *L. stanvellense* vary from locality to locality, and many of them resemble *L. voiseyi* more closely than do the topotypes. The specimens from Bingara figured by Hill (1934, pl. 10, fig. 32,33) have thickened septa, but thickening occurs in both the dissepimentarium and the tabularium. Also in this form the dissepimentarium is much narrower than in *L. voiseyi.* Smith (1920, pl. 3) has figured specimens of a different variety of *L. stanvellense* from Bingara. These figures are not very clear but it is apparent that the axial series of tabellae is flatter and the dissepimentarium is narrower than in *L. voiseyi.* The Bingara material occurs in association with *Aphrophyllum* (but not *Amygdalophyllum*) in a dark coloured limestone "intercalated with Burindi mudstones" (Benson, 1917, p. 242). This, together with the fact that *Aphrophyllum* has been found elsewhere well down in the Lower Burundi mudstones (as I hope to show in a later paper), indicates that the Bingara limestone is probably of Tournaisian age.

Specimens referred to *L. stanvellense* are abundant in the limestone interbedded with

Lower Kuttung rocks at Babbinboon. Several of these specimens have been sectioned for comparative purposes, and there is no doubt that they are closely related to *L. voiseyi*. They may however be distinguished by their much more pronounced and commonly lonsdaleoid dissepimentarium, the absence of two clearly defined series of tabellae and the absence of a thickened counter septum connecting with the columella.

All of the specimens of *L. voiseyi* are preserved in a narrow band toward the base of the oolitic limestone at the top of the Watts, Babbinboon deposit.

Range.—Upper Tournaisian. Species of this type have not previously been recognised in beds older than the Upper Viséan in eastern Australia. It is now apparent that *Lithostrotion* in this area has a wider range than previously realized, and the occurrence of this genus, without the association of *Amygdalophyllum*, can no longer be accepted as evidence of a horizon high in the Dinantian. Further work may show that this species ranges into the Viséan.

REFERENCES

BENSON, W. N., 1917, Geology and petrology of the Great Serpentine Belt of New South Wales: Linnean Soc. New South Wales, Proc., vol. 42, p. 223–45, 250–283, 693–700.

——, & DUN, W. S., 1920, The geology of the Great Serpentine Belt of New South Wales: Pt. IX, Section B: Linnean Soc. New South Wales, Proc., vol. 45, p. 337–374, pl. 18–24.

——, & SMITH, S., 1923, On some rugose corals from the Burindi Series (Lower Carboniferous) of New South Wales: Geol. Soc. London, Quart. Jour., vol. 79, p. 156–171, pl. 8–9.

BOND, G., 1941, Species and variation in British and Belgian Carboniferous Schizophoriidae: Proc. Geol. Assoc., vol. 52, p. 285–303, pl. 21–22.

BRANSON, E. B., et al., 1938, Stratigraphy and paleontology of the Lower Mississippian of Missouri, Pts. I and II: Univ. Missouri Studies, vol. XIII, no. 13–14.

BROWNE, I. A., 1953, *Martiniopsis* Waagen from the Salt Range, India: Royal Soc. New South Wales, Proc., vol. 86, p. 100–107, pl. 9.

BUCKMAN, S., 1908, Brachiopod homemorphy: Geol. Soc. London, Quart. Jour., vol. 64, p. 27–33.

CAMPBELL, K. S. W., 1955, The genus *Phricodothyris* in the Carboniferous of New South Wales: Geol. Mag., vol. 92, p. 374–84, pl. 18.

——, 1956, Some Carboniferous productids from New South Wales: Jour. Paleont. vol. 30, p. 463–480, pl. 48–50, 5 text-fig.

CAREY, S. W., 1934, The geological structure of the Werrie Basin: Linn. Soc. New South Wales, Proc., vol. 59, pt. 5, p. 351–379.

——, 1937, The Carboniferous sequence in the Werrie Basin: Linn. Soc. New South Wales, Proc., vol. 62, pts. 5–6, p. 341–376.

CASTER, K. E., 1939, A Devonian fauna from Columbia: Bull. Am. Paleont., vol. 24, no. 83, p. 1–218, pl. 1–14.

CHU, S., 1933, Corals and brachipods of the Kinlin Limestone: Mon. Nat. Res. Inst. Geol., Nanking (A), vol. 2, p. 1–58, pl. 1–5.

COOPER, G. A., 1944, in SHIMER, H. W., and SHROCK, R. R., Index fossiis of North America: John Wiley & Sons, New York.

CROCKFORD, J., 1947, Bryozoa from the Lower Carboniferous of New South Wales and Queensland: Linn. Soc. New South Wales, Proc., vol. 72, pt. 1, p. 1–48, pl. 1–5.

——, 1951, The development of bryozoan faunas in the Upper Paleozoic of Australia: Linn. Soc. New South Wales, Proc., vol. 76, pts. 3–4, p. 105–122.

DAVIDSON, T., 1857–1863, A monograph of the British Carboniferous Brachiopoda: Palaeont. Soc. Monogr. p. 1–280, pl. 1–55.

DELÉPINE, G., 1941, On Upper Tournaisian goniatites from New South Wales: Ann. Mag. Nat. Hist., ser. 11, vol. 7, p. 386–395, pl. 5.

DEMANET, F., 1934, Les Brachiopodes du Dinantien de la Belgique: Mem. Mus. Hist. Nat. Belgique, no. 61, p. 1–114, pl. 1–10.

DIENER, C., 1899, Anthracolithic fossils of Kashmir and Spiti: Pal. Indica (15) Himalayan fossils, vol. 1, no. 2, p. 1–95, pl. 1–8.

——, 1915, The Anthracolithic faunae of Kashmir, Kanaur and Spiti; Pal. Indica (n.s.), vol. 5, no. 2, p. 1–135, pl. 1–11.

DOBROLYUBOVA, T., 1940, The rugosa corals of the Upper Carboniferous of the Moscow Basin: Trud. Palaeont. Inst. Akad. Nauk. S.S.S.R., vol. 9, fasc. 3, p. 1–88, pl. 1–25.

DRESSER, H., 1954, Contributions to knowledge of the Brazilian Paleozoic, No. 1: Bull. Am. Paleont., vol. 35, no. 149, p. 1–84, pl. 1–8.

DUN, W. S., 1900, Notes on some Carboniferous brachiopods from Clarencetown: Rec. Geol. Survey New South Wales, vol. 7, no. 1, p. 72–88, pls. 21–23.

DUNBAR, C. O., & CONDRA, G. E., 1932, Brachiopoda of the Pennsylvanian System in Nebraska: Nebraska Geol. Survey, Bull. 5, ser. 2, p. 1–377, pl. 1–44.

ETHERIDGE, R., JR., 1891, Carboniferous and Permo-Carboniferous Invertebrata of New South Wales, Part 1, Coelenterata: Mem. Geol. Survey New South Wales, Pal. no. 5, p. 1–64, pl. 1–6.

——, 1892, in Jack, R. L., & Etheridge, R., Jr., Geology and palaeontology of Queensland and New Guinea: Publ. Geol. Survey Queensland, no. 92, p. 1–756, pl. 1–68.

——, 1900, Corals from the Coral Limestone of Lion Creek, Stanwell, near Rockhampton: Geol. Survey Queensland, Bull. 12, p. 1–24, pl. 1–2.

FRECH, F., 1899, Das Carbon (Die Steinkohlen-

formation) Lethaea geonostica: Lethaea paleozoica II.

GALLWITZ, H., 1932, Die Fauna des deutschen Unterkarbons: die Brachiopoden, 3. Teil. Die Orthiden, Strophomeniden und Choneten des Unteren Unterkarbons (Etroeungt): Abh. preuss. geol. Landes., N. F., Heft 141, p. 75–131, pl. 6–8.

GEORGE, T. N., 1927, Studies in Avonian Brachiopoda, I. The Genera *Brachythyris* and *Martinia:* Geol. Mag., vol. 64, p. 106–119.

——, 1931. *Ambocoelia* Hall, and certain similar British Spiriferidae: Geol. Soc. London, Quart. Jour., vol. 87, p. 30–61, pl. 3–5.

——, 1932, The British Carboniferous reticulate Spiriferidae: Geol. Soc. London, Quart. Jour., vol. 88, p. 516–575, pl. 31–35.

——, 1952, Tournaisian facies in Britain: Rept. Int. Geol. Cong., XVIII, G. B. 1948, pt. 10, p. 34–41.

——, 1954, Pre-Seminulan Main Limestone of the Avonian in Breconshire: Geol. Soc. London, Quart. Jour., vol. 110, pt. 3, p. 283–322, pl. 12.

——, & PONSFORD, D. R. A., 1938, Notes on the morphology of *Schizophoria:* Leeds Geol. Assoc., Trans., vol. 5, pt. 4, p. 227–245, pl. 5.

GIRTY, G. H., 1908, Guadalupian fauna: U. S. Geol. Survey, Prof. Paper 58, 651 p., 31 pl.

GORSKY, I. I., & TIMOFEEVA, I. L., 1939, Fauna of the Coal Bearing Series of the Kizel Districts: Trans. Centr. Geol. Props. Inst. Moscow, vol. 111, p. 1–143, pl. 1–7.

HALL, J., 1867, Natural History of New York, Pt. 6 Palaeontology: vol. 4, p. 1–428, pl. 1–63.

HAYASAKA, I., 1924, On the fauna of the Anthracolitic Limestone of Omi-mura in the western part of Echigo: Sci. Rep. Tohoku Univ., voi. 8, no. 1, p. 1–83, pl. 1–7.

HILL, D., 1934, The Lower Carboniferous corals of Australia: Royal Soc. Queensland, Proc., vol. 45, p. 63–115, pl. 7–11.

——, 1939–40, A monograph on the Carboniferous rugose corals of Scotland: Mon. Palaeont. Soc. London, pts. 2 and 3, p. 99–204, pl. 3–11.

——, 1948, The Distribution and Sequence of Carboniferous Coral Faunas: Geol. Mag., vol. 85, no. 3, p. 121–149.

——, 1956, Treatise on Invertebrate Palaeontology: pt. F. Coelenterata.

HUDSON, R. G. S., 1936, The development and septal notation of the Zoantharia Rugosa (Tetracoralla): Yorkshire Geol. Soc., Proc., vol. 23, p. 68.

JACK, R. L., & ETHERIDGE, R., JR., 1892, The geology and paleontology of Queensland and New Guinea: Geol. Survey Queensland, Publ. 92, p. 1–756, pl. 1–68.

KINDLE, E. M., 1909, The Devonian of the Ouray limestone: U. S. Geol. Survey, Bull. 391, p. 1–60, pl. 1–10.

KONINCK, L. G., DE, 1842–4, Description des animaux fossiles du terrain carbonifère de Belgique: p. 1–649, pl. 1–69, Liege.

——, 1876, Descriptions of the Palaeozoic fossils of New South Wales: Mem. Geol. Survey New South Wales, Palaeont., no. 6, p. 1–298, pl. 1–14.

LEWIS, H. P., 1929, On the Avonian Coral *Caninophyllum* gen. nov., and *C. archiaci* (Edwards and Haime): Ann. Mag. Nat. Hist., vol. 3, ser. 10, p. 456–468, pl. 11–12.

MAILLIEUX, F., 1932, La faune de l'assise de Winenne: Mem. Mus. roy. Hist. Nat. Belg., no. 51.

——, 1935, Contribution a la connaissance de quelques brachiopodes et pelecypodes Devoniens: Mem. Mus. roy. Hist. Nat. Belg., no. 70.

MANSUY, H., 1912, Etude geologique du Yunnan oriental. II Palaeontologie: Mem. Serv. Geol. Indo-Chine, vol. 1, pt. 2, p. 1–146, pl. 1–25.

MARTIN, W., 1809, Petrificata Derbiensia: Wigan, p. 1–102, pl. 1–52.

MAXWELL, W. G. H., 1950, An Upper Devonian brachiopod (*Cyrtospirifer reidi* sp. nov.): Univ. Queensland Papers, vol. 3, no. 12, p. 1–8, pl. 1.

——, 1951, Upper Devonian and Middle Carboniferous brachiopods of Queensland: Univ. Queensland Papers, vol. 3, no. 14, p. 1–27, pl. 1–4.

——, 1954, Upper Palaeozoic formations in the Mt. Morgan District-Faunas: Univ. Queensland Papers, vol. 4, no. 5, p. 1–69, pl. 1–6.

MCCOY, F., 1847, On the fossil botany and zoology of the rocks associated with coal in Australia: Ann. Mag. Nat. Hist., vol. 20, p. 145–157, 226–236, 298–331.

MINATO, M., 1951, On the Lower Carboniferous fossils of the Kitakami Massif, Northeast Honsyu, Japan: Jour. Faculty Sci., Hokkaido Univ., ser. 4, vol. 7, no. 4, p. 355–382, pl. 1–5.

——, 1952, A further note on the Lower Carboniferous fossils of the Kitakami Mountainland, North-east Japan: Jour. Faculty Sci., Hokkaido Univ., ser. 4, vol. 8, no. 2, p. 136–174, pl. 1–11.

MUIR-WOOD, H. M., 1928, The British Carboniferous Producti, II. *Productus (sensu stricto); semireticulatus* and *longispinus* groups: Mem. Geol. Survey Gt. Britain, Palaeont., vol. 3, pt. 1, p. 1–217. pl. 1–12.

——, 1929, The classification of the British Carboniferous brachiopod subfamily Productinae: Ann. Mag. Nat. Hist., vol. 5, p. 100–108.

——, in Garwood, E. J., 1931, The Teudian Beds of Northern Cumberland and Roxburgshire East of the Liddel Water: Geol. Soc. London, Quart. Jour., vol. 87, pt. 1, p. 97–159, pl. 7–14.

——, 1948, Malayan Lower Carboniferous fossils: British Mus. Nat. Hist., p. 24–77, pl. 1–10.

——, 1951, The Brachiopoda of Martin's "Petrificata Derbiensia": Ann. Mag. Nat. Hist., ser. 12, vol. 4, p. 79–118, pl. 3–6.

——, & STUBBLEFIELD, C. J., 1951, Proposed use of the plenary Powers to validate the trivial names of two nominal species of the Class Anthozoa, and of eight nominal species of the Class Brachiopoda, published by William Martin in 1809 in the work entitled

"Petrificata Derbiensia," and matters incidental thereto: Bull. Zool. Nomen, vol. 6, pt. 1, p. 7–18,

NALIVKIN, A. V., 1937, Brachiopods of the Uperp and Middle Devonian and Lower Carboniferous of North-Eastern Kazakhstan: Trans. Cent. Geol. Prosp. Inst., U.R.S.S., vol. 99, p. 1–200, pl. 1–39.

NORTH, F. J., 1920, On *Syringothyris* Winchell and certain Carboniferous Brachiopoda referred to *Spiriferina* d'Orbigny: Geol. Soc. London, Quart. Jour., vol. 76, p. 162–227, pl. 11–13.

PAECKELMANN, W., 1930, Die Brachiopoden des deutschen Unterkarbons, I. Die Orthiden, Strophomeniden und Chonetiden des Mittleren und Oberen Unterkarbons: Abh. Preuss. Geol. Landesanst., (n.f.), vol. 122, p. 1–326, pl. 1–24.

——, 1931, Die Fauna des deutschen Unterkarbons, II: Abh. Presuss. Geol. Landesanst. (n.f.), vol. 136, p. 1–440, pl. 1–41.

——, 1942, Beiträge zur Kenntnis devonischer Spiriferen: Abh. Reich. für Bodenforschung, (n.f.), Heft. 197, p. 1–188, pl. 1–8.

PARKINSON, D., 1954, Quantitative studies of brachiopods from the Lower Carboniferous reef limestones of England, I. *Schizophoria resupinata* (Martin): Jour. Paleont., vol. 28, no. 3, p. 367–381.

——, 1954, Quantitative studies of brachiopods from the Lower Carboniferous reef limestones of England, III. *Pugnax acumunatus* (J. Sowerby) and *P. mesogonus* (Phillips): Jour. Paleont., vol. 28, no. 5, p. 668–676.

PRENDERGAST, K. L., 1935, Some Western Australian Upper Palaeozoic Fossils: Royal Soc. West. Australia, Jour., vol. 21, p. 9–35, pls. 2–4.

——, 1943, Permian Productinae and Strophalosiinae of Western Australia: Royal Soc. West. Australia, Jour., vol. 28, p. 1–73, pl. 1–6.

RAMSBOTTOM, W. H. C., 1952, The fauna of the Cefn Coed Marine Band in the Coal Measures at Aberbaiden, near Tondu, Glamorgan: Bull. Geol. Survey Great Britain, no. 4, p. 8–32.

REED, F. R. C., 1927, Palaeozoic and Mesozoic Fossils from Yunnan: Pal. Indica, n.s., vol. 10, p. 1–291, pl. 1–20.

——, 1948, Notes on some Carboniferous Spiriferidae from Fife: Ann. Mag. Nat. Hist., vol. 1, ser. 12, p. 449–487, pl. 7–12.

ROTAI, A., 1931, Brachiopods and stratigraphy of the Lower Carboniferous of the Donetz Basin: Trans. Cent. Geol. Prosp. Inst., U.R.S.S., vol. 73, p. 35–144, pl. 1–10.

SALEE, A., 1910, Contribution a l'étude des Polypiers du Calcaire Carbonifère de la Belgique. Le Genre *Caninia*. Soc. Belg. Geol. Pal. Hydrol. Brussels, Nouv. Mem., Mem. 3, p. 1–62, pl. 1–9.

SARYCHEVA, T. G., 1949, Morphology, ecology, and evolution of Carboniferous productids near Moscow (genera *Dictyoclostus*, *Pugilis* and *Antiquatonia*): Trudy Palaeont., Inst., Acad. Nauk S.S.S.R., vol. 18, p. 1–304, pl. 1–36.

——, & SOKOLSKAYA, A. N., 1952, Index of Palaeozoic brachiopods from the sub-Moscow Basin: Trudy Palaeont., Inst. Acad. Nauk. S.S.S.R., vol. 38, p. 1–305, pl. 1–71.

SCHUCHERT, C., 1928, Review of the late Paleozoic formations and faunas, with special reference to the Ice Age of Middle Permian Time: Geol. Soc. Am., Bull., vol. 39, p. 769–886.

——, & COOPER, G. A., 1932, Brachiopod genera of the orders Orthoidea and Pentameroidea: Peabody Mus. Nat. Hist., Mem., vol. 4, pt. 1, p. 1–270, pl. 1–29.

SHEARSBY, A. J., 1911, The geology of the Yass District: Rept. Australian Assoc. Advancement Sci., vol. 13, p. 106–119.

SMITH, S., 1920, On *Aphrophyllum hallense* Gen. et. Sp. Nov., and *Lithostrotion* from the Neighbourhood of Bingara, N.S.W.: Royal Soc. New South Wales, Jour. and Proc., vol. 54, p. 51–65, pl. 2–5.

——, 1925, Notes upon the small species of *Chonetes* found in the Lower Carboniferous around Bristol: Geol. Mag., vol. 62, p. 85–88.

SOKOLSKAYA, A. N., 1941, Lower Carboniferous and Devonian-Carboniferous brachiopods of the Moscow Basin (Tschernyschino, Upa and Malevka-Murajevnia Beds). Pt. 1, Spiriferidae Trav. Inst. Palaeont. Moscow, vol. 12, no. 2, p. 1–139, pl. 1–12.

——, 1950, Chonetidae of the Russian Platform: Palaeont. Inst. Acad. Nauk. Trudy, S.S.S.R., vol. 27, p. 1–108, pl. 1–13.

——, 1954, Strophomenidae of the Russian Platform: Trudy Palaeont. Inst. Acad. Nauk. S.S.S.R., vol. 51, p. 1–187, pl. 1–18.

STAINBROOK, M. A., 1947, Brachiopoda of the Percha shale of New Mexico and Arizona: Jour. Paleont., vol. 21, no. 4, p. 297–328, pl. 44–47.

——, 1945, Brachiopoda of the Independence shale of Iowa: Geol. Soc. Am., Mem. 14, p. 1–74, 6 pl.

STEHLI, F. G., 1954, Lower Leonardian Brachiopoda of the Sierra Diablo: Am. Mus. Nat. Hist., Bull., vol. 105, art. 3, p. 263–358, pl. 17–27.

SUTTON, A. H., 1938, Taxonomy of Mississippian Productidae: Jour. Paleont., vol. 12, p. 537–569, pl. 62–66.

THOMAS, I., 1910, The British Carboniferous Orthotetinae: Mem. Geol. Survey Great Britain, Palaeont., vol. 1, pt. 2, p. 83–134. pl. 13.

——, 1914, The British Carboniferous Producti, I. Genera *Pustula* and *Overtonia*. Mem. Geol. Survey Great Britain, Palaeont., vol. 1, pt. 4, p. 197–366, pl. 17–20.

TIEN, C. C., 1938, Devonian Brachiopoda of Hunan: Pal. Sinica. (n.s.), vol. 8, no. 4, p. 1–147, pl. 1–22.

TING, V. K., 1931, On the stratigraphy of the Fengninian System: Geol. Soc. China, Bull., vol. 10, p. 31–48, pl. 1–2.

TOLMACHOFF, I. P., 1924, Faune du clacaire Carbonifère du Bassin houiller de Kousnetzk, I: Mater. Geol. gen. appl. Leningrad, vol. 25, p. 1–320, 12 pl.

——, 1926, Lower Carboniferous fauna, Kuznetzk Coal Field, Altai, Siberia: Am. Jour. Sci., ser. 5, vol. 11, p. 411–422.
——, 1931, Faune du Calcaire Carbonifère du Bassin houiller de Kousnetzk, II: Mater Geol. gen. appl. Leningrad, vol. 25, p. 321–663, 11 pl.
VAUGHAN, A., 1903, Notes on the corals and brachiopods obtained from the Avon Section and preserved in the Stoddart Collection: Bristol Nat. Soc., Proc., (n.s.), vol. 10, p. 90–134, pl. 1–2.
——, 1905, The palaeontological sequence in the Carboniferous Limestone of the Bristol Area: Geol. Soc. London, Quart. Jour., vol. 61, p. 181–308, pl. 22–29.
——, 1915, The correlation of Dinantian and Avonian: Geol. Soc. London, Quart. Jour., vol. 71, pt. 1, p. 1–52, pl. 1–7.
WELLER, J. M., et al., 1948, Correlation of the Mississippian formations of North America: Geol. Soc. Am. Bull., vol. 59, no. 2, p. 91–196.
WELLER, S., 1914, The Mississippian brachiopods of the Mississippi Valley Basin: Illinois State Geol. Survey, Monograph I, p. 1–508, pl. 1–83.
WILLIAMS, A., 1951, Llandovery brachiopods from Wales with special reference to the Llandovery District: Geol. Soc. London, Quart. Jour., vol. 107, pt. 1, p. 85–134, pl. 3–8.
——, 1953, The classification of the strophomenid brachiopods: Washington Acad. Sci., Jour., vol. 43, p. 1–13.
YANISHEVSKY, M., 1918, Materials for the study of the Lower Carboniferous fauna of Ferghana: Mem. Com. Geol. Petrograd, vol. 162, p. 1–145, pl. 1–8.

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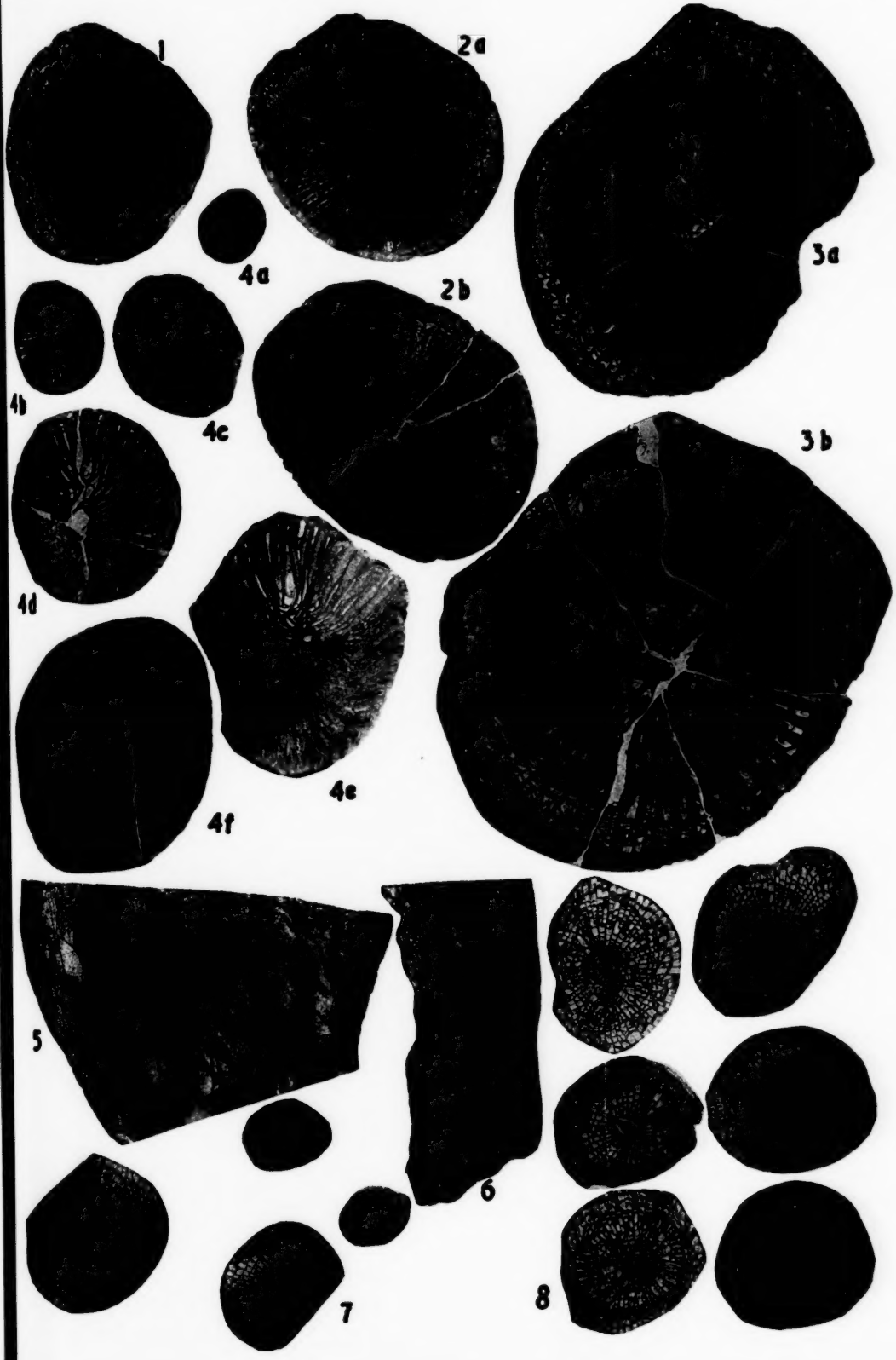
EXPLANATION OF PLATE 17

(All specimens ×1.8 approx. Specimen numbers refer to the University of New England Collections unless otherwise stated.)

FIG. *1–5*—***Caninophyllum sumphuens*** (Etheridge). *1*, holotype, transverse section of a young individual cut at the early ephebic stage, F. 46215 Australian Museum Collections; *2a-f*, serial transverse sections of an individual, F. 2934; *3a,b*, two transverse sections of a young individual, F. 2936; *4a,b*, two transverse sections of an older individual, F. 2930; *5*, vertical section through the fossula, F. 2935. (In all of these specimens the dissepimentarium is more or less eroded off.) (p. 92)

6–8—***Lithostrotion voiseyi***, n. sp. *6*, vertical section, F. 2893; *7*, holotype, transverse section of a small part of a corallum, F. 2892; *8*, transverse sections of a number of isolated individuals, F. 2933. (p. 94)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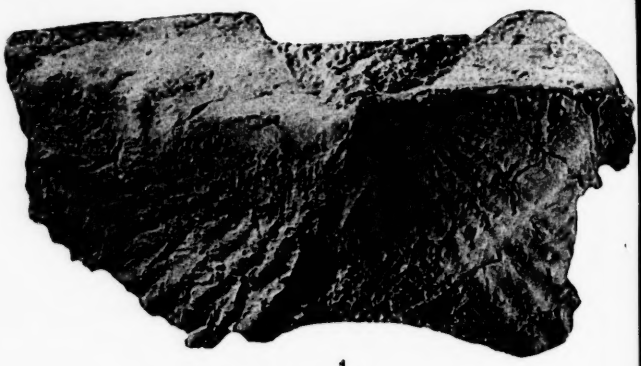

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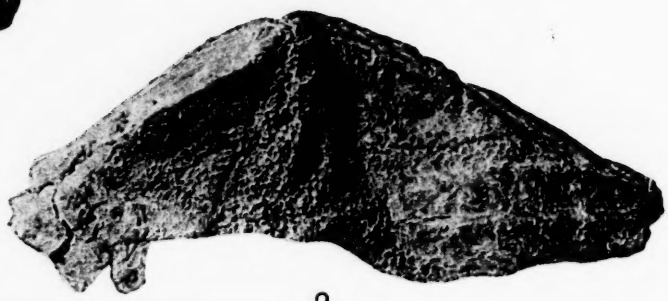

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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 1, P. 99–104, PL. 18, 3 TEXT-FIG., JANUARY 1957

NEW SYRINGOTHYRID BRACHIOPODS FROM MENDOZA, ARGENTINA

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ABSTRACT—A collection of Lower Carboniferous brachiopods from the sandstones and conglomerates of the Sistema del Imperial, Mendoza, has furnished the material for this study. *Septosyringothyris* aff. *S. keideli* is characterized by a thick euseptum and high cardinal area. In *Syringothyris feruglioi*, n. sp., a transversely coiled syrinx and divergent dental lamellae are the outstanding features.

INTRODUCTION

IN 1944, Egidio Feruglio examined a collection of fossils discovered by R. Dessanti in the coarse sandstones and conglomerates of the Sistema del Imperial, Departmento San Rafael, Mendoza. He referred them to a species comparable with *Syringothyris keideli* Harrington. A new examination of the specimens supplemented by transverse sections of the ventral valve shows some of them to belong to *Septosyringothyris* Vandercammen, 1955, characterized by the presence of a euseptum connecting the syrinx with the floor of the valve; the remainder are referred to *Syringothyris feruglioi*, n. sp.

The writer wishes to express his gratitude to Professor T. Neville George for reading the manuscript and for help and guidance throughout the work. Some problems of illustration were discussed with Dr. J. Weir; to him and Mr. A. Ferguson the writer expresses his indebtedness.

This work has been carried out during the tenure of a British Council Scholarship.

SYSTEMATIC DESCRIPTIONS

SEPTOSYRINGOTHYRIS aff. S. KEIDELI (Harrington)

Text-fig. 1a-k; 3a-d

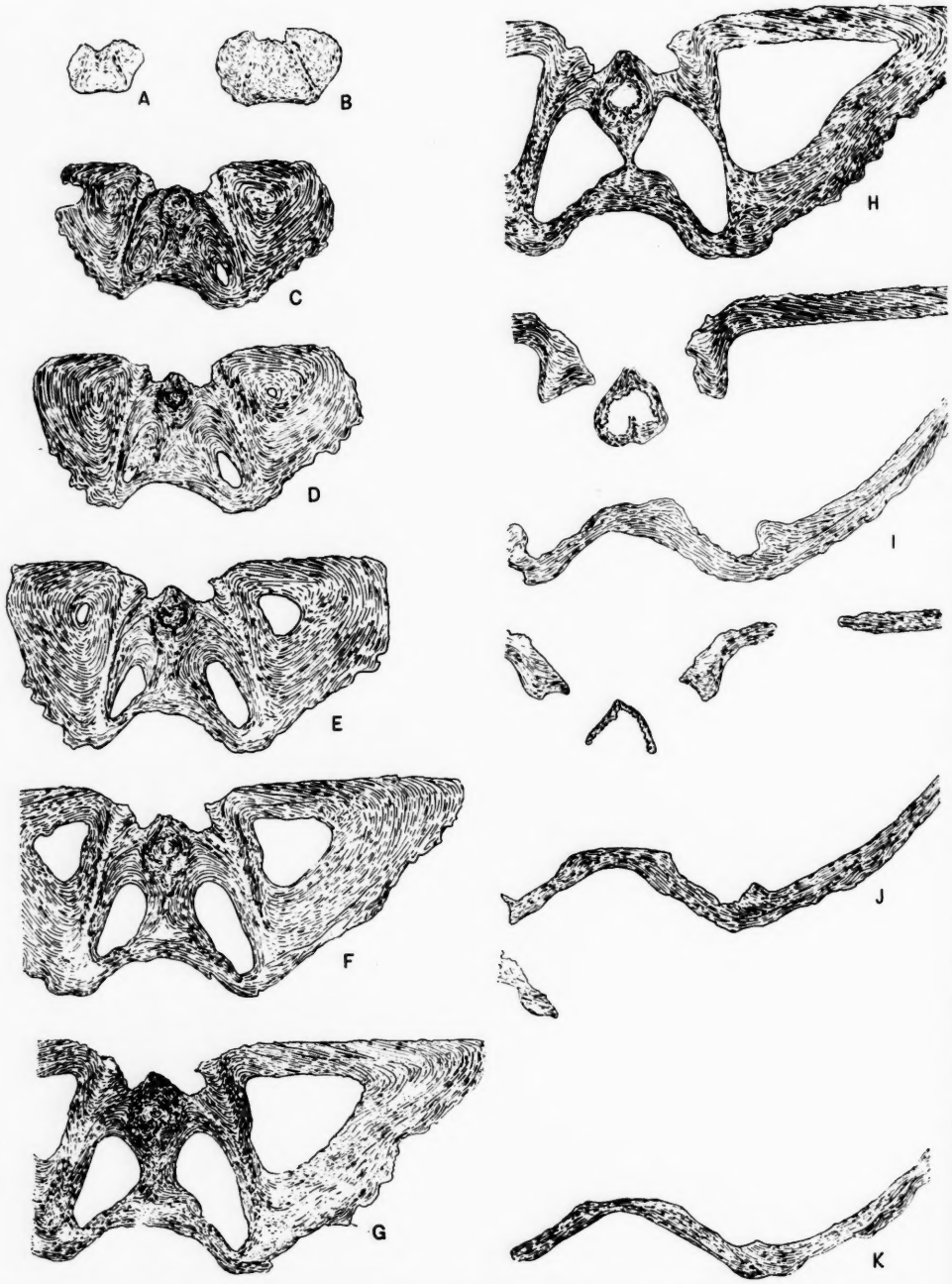
Syringothyris keideli HARRINGTON, in Keidel & Harrington, 1938.
Syringothyris keideli Harrington, DESSANTI, 1945, p. 214.

Description of ventral valve.—External characters: Area slightly concave. Apical angle 120°. Delthyrial angle 30°. Delthyrium triangular, width one fifth the hinge line. Sulcus U-shaped, not very deep and not sharply defined from the lateral slopes; the median line along its floor is slightly convex. Lateral slopes with 10 to 12 low rounded costae, badly preserved, separated by shallow and narrower furrows.

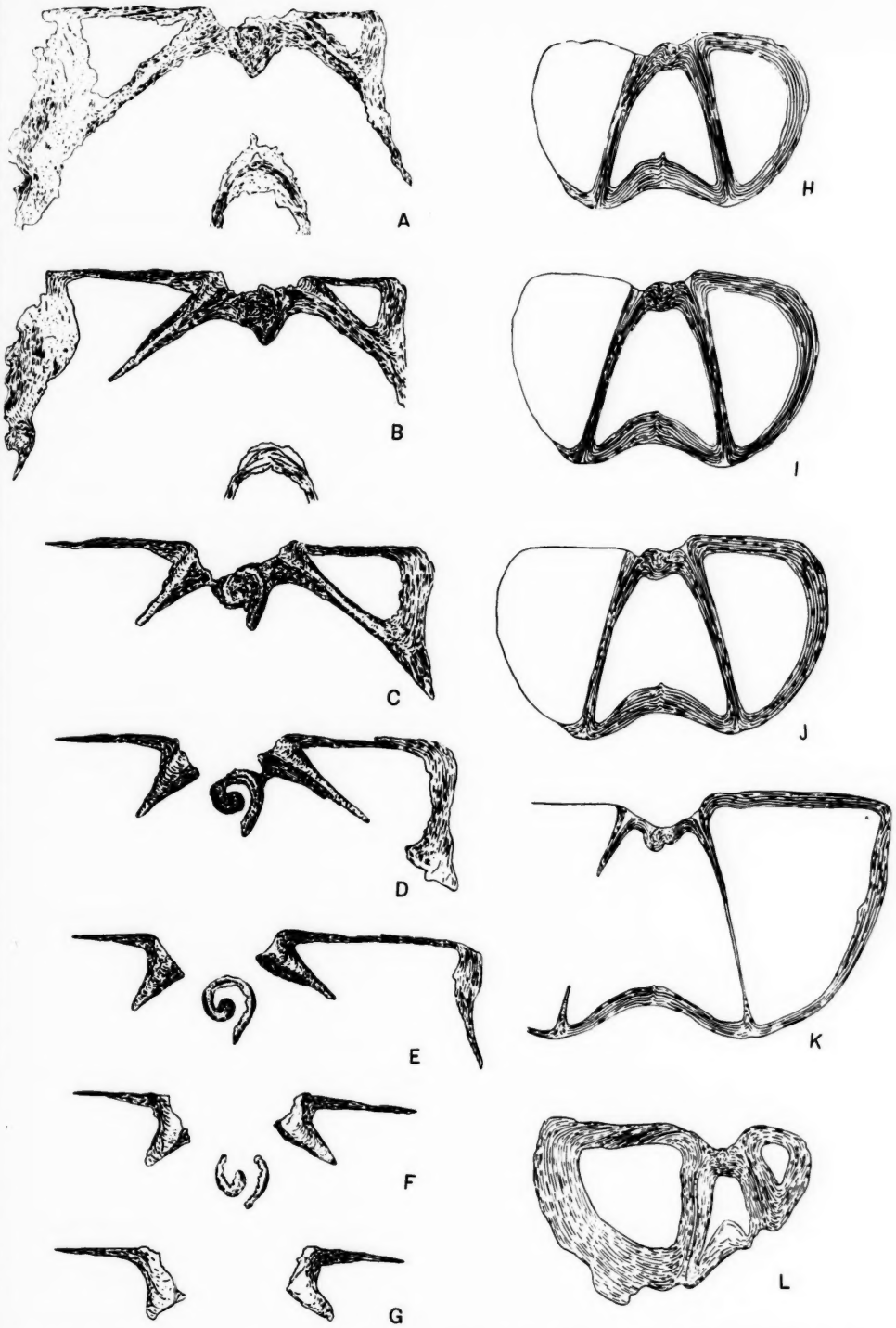
Internal characters: Dental lamellae strong, divergent at about 30° towards the floor of the valve, in cross section extending along the floor of the valve up to 11 mm. from the apex. Beyond that they have concave anterior edges. The inferior part extends as a crest along the floor of the valve, for a shorter distance than the upper part which continues as a dental ridge up to the hinge line. Transverse plate connecting dental lamellae. Low median ridge on upper surface of transverse plate triangular in cross section. Syrinx slightly asymmetrical in transverse section, one third the delthyrial opening in diameter, cylindrical anteriorly but becoming compressed laterally and elongated dorsoventrally along its median portion and having an inverted cardiform shape at its distal end. Internally the syrinx has 12 to 15 sharply angular ridges arranged longitudinally, about one tenth the diameter of the syrinx in height. The inferior ridges are sometimes longer and branched. The

EXPLANATION OF PLATE 18

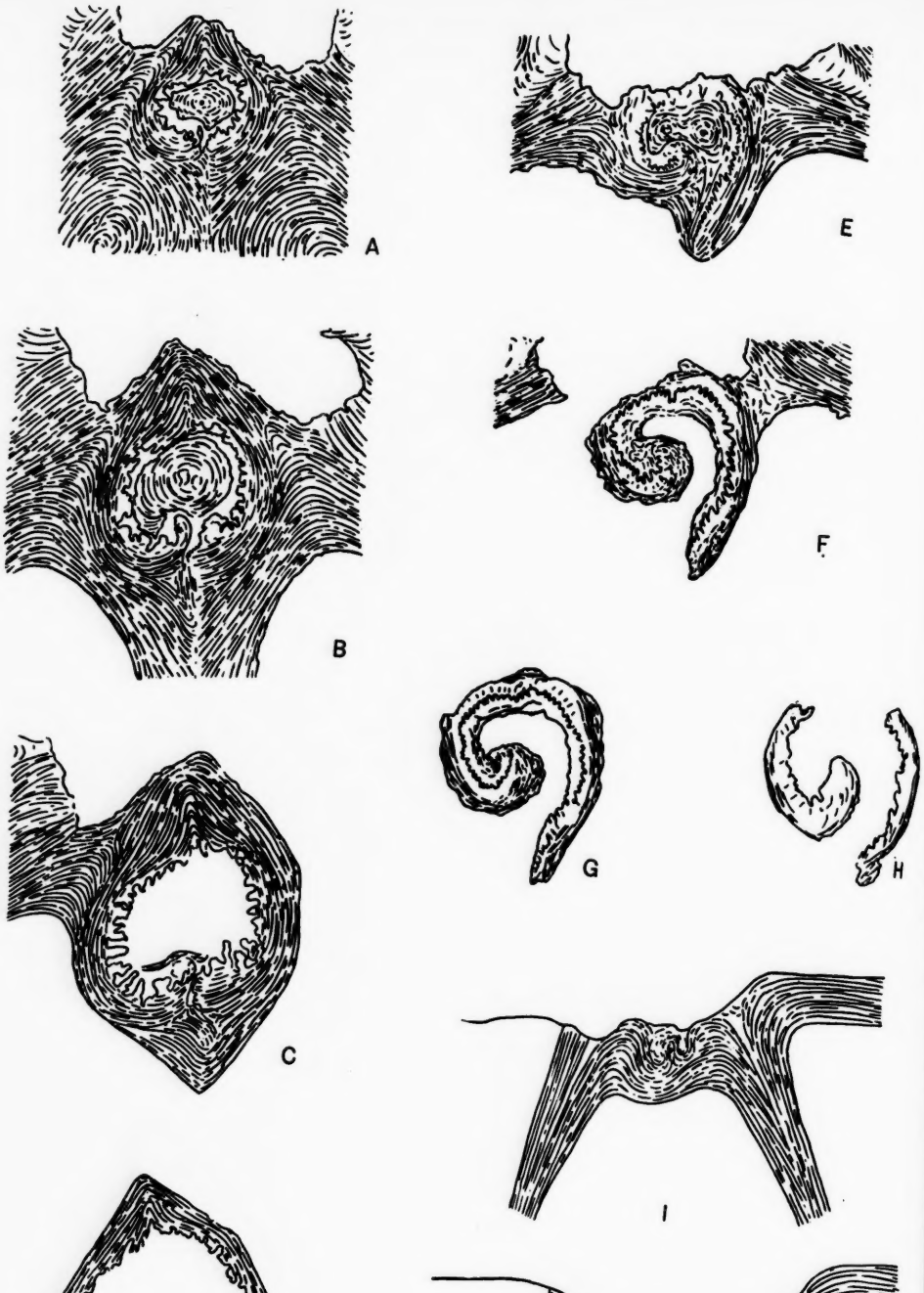
FIG. *1–4*—*Syringothyris feruglioi*, n. sp. *1,2*—Holotype, ventral valve, posterior view and view of Cardinal area; *3,4*, Paratype ventral valve, lateral and posterior views. All ×1.1.
5–7—*Syringothyris feruglioi*, n. sp., Tangential, oblique and transverse sections showing punctations in fibrous layer. Approx. ×192.



TEXT-FIG. *1*—Sections across the ventral valve of *Septosyringothyris* aff. *S. keideli* (Harrington). ×2.5. Distance of sections from apex in mm.: A, 1.5; B, 1.9; C, 6.4; D, 7.0; E, 8.2; F, 9.5; G, 10.4; H, 12.0; I, 14.0; J, 17.2; K, 19.0.



TEXT-FIG. 2—Sections across the ventral valve. ×2.5. A-G, *Syringothyris feruglioi*, n. sp.; H-K, *Syringothyris cuspidata* (Martin) from Cork, Ireland; L, *Syringothyris* aff. *S. cuspidata* (Martin) from Titterstone-Clee Hill. Distance of sections from apex in mm.: A, 3.4, B, 4.0; C, 5.4; D, 6.2; E, 6.9; F, 7.8; G, 9.0; H, 4.6; I, 5.0; J, 5.2; K, 9.0; L, 3.0.



TEXT-FIG. *3*—Cross sections of the syrinx, ×7.5. A-D, *Septosyringothyris* aff. *S. keideli* (Harrington); E-H, *Syringothyris feruglioi*, n. sp.; J,K, *Syringothyris cuspidata* (Martin) from Cork. Distance of sections from apex in mm.: A, 7.1; B, 10.0; C, 12.0; D, 16.0; E, 4.1; F, 6.0; G, 6.3; H, 7.8; I, 5.1; J, 8.6.

syrinx is open only on its ventral side when it approaches the hinge line. Posteriorly its inner flanks are embedded in later growth. The flanks become thinner and shorter anteriorly until the syrinx disappears as a small inverted V just before reaching the hinge line. Euseptum thick, extending anteriorly to the same distance as the dental lamellae, connecting the syrinx with the floor of the valve, wrapping around and enclosing the syrinx longitudinally along its inferior portion. Anteriorly the euseptum ends with a concave edge in the same way as the dental lamellae.

Shell structure.—With the aid of a powerful lens very small punctations can be observed on certain parts of the exfoliated shell surface. They appear as small rounded pits, distributed irregularly on the surface. The diameter of these tubes varies between 0.007–0.014 mm. The apical cavity is completely filled posteriorly up to 7 mm. from the umbo with shell growth, the dental lamellae and euseptum are also thickened.

Dimensions.—

Height of area	20 mm.
Width of area	50 mm.
Width of delthyrium	11 mm.
Apical angle	120°
Delthyrial angle	30°

Remarks.—The form now described agrees with *Syringothyris keideli* Harrington (1938) in possessing a thick euseptum (Harrington considered the partition in the apical cavity as "apical callosity"). Nevertheless a more abundant collection may show it to fall into a new species, for it differs from *S. keideli* in the smaller number of ribs and the narrower apical angle. The height of the area is also proportionally smaller in Harrington's species—about one fourth to one fifth the width of the hinge line, against one half to one third in the present one. On the other hand, the present form is closely similar to one of the forms of *Septosyringothyris demaneti* Vandercammen (1955), in number of costae and in shape, but the area is higher and the delthyrial angle is smaller. Also no fine grooves ("petit sillons, microrainures") are observed; but this may be due to preservation.

Occurrence.—Sandstones and conglomerates of the Sistema del Imperial, Arroyo Imperial, Departmento San Rafael Mendoza; Lower Carboniferous.

SYRINGOTHYRIS FERUGLIOI, n. sp.
Pl. 18, fig. 1–7; Text-fig. 2 a-g; 3 e-h

Syringothyris keideli Harrington, DESSANTI, 1945, p. 214.

Diagnosis.—Shell syringothyroid in aspect. Flat lateral slopes with 12 to 14 costae. Ventral interior with highly divergent dental lamellae and a coiled syrinx.

Description of ventral valve.—External characters: Pyramidal in form. Area flat or nearly flat, height one third its width. Apical angle 120°. Delthyrium triangular, width slightly less than height. Sulcus well defined, U-shaped, smooth. Lateral slopes flat, with 12 to 14 costae, all starting near the beak and not bifurcated. Costae rounded and separated by narrow rounded furrows. Shell structure finely punctate.

Internal characters: Relatively thin dental lamellae, strongly divergent, around 120° in transverse section, extending 6 mm. towards the anterior margin from the umbo, then running as dental ridges up to the hinge line. Euseptoid short in height, extending for 3 mm. near the umbo. Transverse plate thick, slightly convex upwards, extending one half the distance from the umbo to the hinge line. Dorsal surface of plate with a ridge-like process near the apex, triangular in section. Syrinx around one half the delthyrial opening in section, running free from transverse plate beyond one half its length onwards, but not extending beyond hinge line; spiral in transverse section, left flank of "tube" coiled ventrally, right one not so curved and extending downwards. Internally both flanks of syrinx bear well developed long small longitudinal ridges, each about one fifth the diameter of the syrinx. Tube filled up posteriorly with shell growth.

Shell structure.—The fibrous layer is traversed by very fine punctations oblique to the fibres. They appear in the shell surface as very small pits with no definite pattern of arrangement. The diameter of the tubes varies between 0.007 and 0.014 mm. The distance between them is also variable, being in average six to ten times the diameter of a tube (Pl. I, fig. 5–7).

Dimensions.—

	Holotype	Paratype
Height of area	24 mm.	17 mm.
Width of area	67 mm.	61 mm.
Width of delthyrium	19 mm.	16 mm.
Apical angle	123°	120°
Delthyrial angle	45°	40°

Remarks.—The form is characterized by a large coiled syrinx not extending beyond the hinge line, and by possessing highly divergent dental lamellae. It differs from British and Irish Carboniferous species in the smaller number of costae, the obtuse apical angle and the greater divergence of the dental lamellae. In Text-fig. 2 sections of *Syringothyris cuspidata* (Martin) from Cork and *S.* aff. *S. cuspidata* from the Oreton limestone (Z Zone) of Titterstone-Clee Hill, are shown. The dental lamellae of the first are very thin and not so divergent as in the Argentine species. The syrinx is proportionately smaller in the Irish species. *Syringothyris keideli* Harrington (Leanza, 1945, p. 249) from San Juan, Argentina, according to the description is a true *Syringothyris*, as no sign of a euseptum can be found in this specimen. On the other hand *S. keideli* and *S. keideli* var. *erina* Leanza (1948, p. 242) cannot as yet be compared with the present species, their internal structure not being known.

Repository.—Holotype and paratype are deposited in the collection of the Direccion Nacional de Mineria, Buenos Aires, Argentina.

Occurrence.—Sandstones and conglomerates of the Sistema del Imperial, Arroyo Imperial, Departmento San Rafael, Mendoza, Argentina; Lower Carboniferous.

REFERENCES

CARPENTER, W., 1867, On the shell structure of *Spirifer cuspidatus* and of certain allied Spiriferidae: Ann. Mag. Nat. Hist., ser. 3, vol. 20, p. 68.

DAVIDSON, T., 1863, British fossil Brachiopoda: Paleont. Soc. Mon., vol. 2.

——, 1867, Perforate and imperforate Brachiopoda: Geol. Mag., vol. 4, p. 311–15, pl. 14.

DESSANTI, R. N., 1945, Sobre el hallazgo del Carbónico marino en el Arroyo Imperial de la Sierra Pintada (Depto. San Rafael, Prov. de Mendoza): Notas Mus. La Plata, vol. 10, geol. no. 42, p. 205–20.

FREDERICKS, G., 1926, Tabula synoptica Familiae Spiriferidarum King: Bull. Acad. Sci. U.S.S.R., ser. 6, vol. 20, no. 5–6, p. 393–422.

——, 1927, Der Apikalapparat der Brachiopoda testicardines (Morphologische Nomenklatur) Neues Jahrbuch., Beil.-Band 57, Abt. B., p. 1–11.

GIRTY, G. H., 1929, The fauna of the middle Boone near Batesville, Arkansas: B, U. S. Geol. Surv. Prof. paper 154, p. 73–103. 4 pl.

KEIDEL, H., & HARRINGTON, H. J., 1938, On the discovery of Lower Carboniferous tillites in the Precordiellera of San Juan: Geol. Mag., vol. 75, p. 103–29.

KING, W., 1868, A monograph of *Spirifer cuspidatus* Martin: Ann. Mag. Nat. Hist., ser. 4, vol. 2, p. 1–23. pl. 2–3.

LEANZA, A. F., 1945, Braquiópodos carboníferos de la Quebrada de la Herradura al N.E. de Jachal, San Juan: Notas Mus. La Plata, vol. 10, paleont. no. 86, p. 277–314.

——, 1949, Braquiópodos y pelecípodos carboníferos de la Prov. de La Rioja: Rev. Mus. La Plata, vol. 3, sec. paleont., p. 237–264.

MEEK, F. B., 1868, On the punctate shell structure of *Syringothyris:* Geol. Mag., vol. 4, p. 315–6.

NORTH, F. J., 1913, On the genus *Syringothyris* Winchell: Geol. Mag., vol. 10, p. 393.

——, 1920, On *Syringothyris* Winchell and certain Carboniferous Brachiopoda referred to *Spiriferina* d'Orbigny: Geol. Soc. London, Quart. Jour., vol. 76, pt. 2, p. 162–227.

PAECKELMANN, W., 1931, Versuch einer zusammenfassenden Systematik der Spiriferidae King: Neues Jahrbuch, Beil.-Band 67, Abt. B, p. 1–64.

SCHUCHERT, C., 1890, On *Syringothyris* Winchell and its American species: N. Y. State Geol., 9th Ann. Rept., p. 230,

VANDERCAMMEN, A., 1955, *Septosyringothyris demaneti* nov. gen. nov. sp. un syringothyride nouveau de Dinantien de la Belgique: Inst. Royal Sci. Nat. Belgique. Bull., vol. 31, no. 30.

——, 1955a, A propos des perforations du test de *Syringothyris* et des genres voisins: Pub. Ass. Etud. Paleont. Bruxelles, No. 21. Hors. serie V VIII, p. 385–398.

WELLER, S., 1914, The Mississippian Brachiopoda of the Mississippi Valley Basin: Geol. Surv. Illinois, Mon. no. 1, 508 p.

MANUSCRIPT RECEIVED APRIL 18, 1956.

JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 1, P. 105–128, PL. 19, 9 TEXT-FIG., JANUARY 1957

ONTOGENETIC DEVELOPMENT OF TWO OLENELLID TRILOBITES[1]

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ABSTRACT—Complete silicified ontogenetic series for the cephalon and hypostome of *Olenellus gilberti* Meek and *Paedeumias clarki* Resser provide the first record of the full development of these features in olenellid trilobites. Five morphologically distinguishable developmental stages including at least 29 instars are identifiable for each species. Anaprotaspid and metaprotaspid stages are not recognized.

Procranidial spines are present on the cephalon only in the first three developmental stages. They maintain a constant position on the anterolateral margin until they disappear. Intergenal spines representing the pleural extensions of the preoccipital segment are present throughout development. They are prominent in the first three developmental stages, are considerably reduced during the fourth stage and are present only as nubs in the fifth stage. Genal spines seem to develop from the border in the third developmental stage.

Statistical observations show the existence of curvilinear growth for specimens with glabellar lengths up to 2 mm. and rectilinear growth for larger specimens.

A suggested merocyclic condition of single macropleural segments alternating with two normal segments in the anterior portion of these trilobites is evidence for considering the olenellid cephalon to be composed of at least eight primary dorsal segments.

Hypostomes from young individuals have prominent, slender anterior wings, a narrow anterior lobe of the middle body, and 13 distinct spines along the lateral and posterior margins. Hypostomes from adults have bluntly rounded anterior wings, a prominent inflated anterior lobe of the middle body and the marginal spines reduced to nubs. Hypostomes of *O. gilberti* and *P. clarki* are indistinguishable.

SILICIFIED Lower Cambrian trilobites were discovered in 1949 in the Combined Metals bed of the Pioche shale on the east side of the Pioche Hills in the Pioche Mining district, Lincoln County, Nevada by C. W. Merriam of the U. S. Geological Survey. Additional material from two new localities at the same stratigraphic level about eight miles west of Merriam's locality, on the west side of the Highland Range, Lincoln County, Nevada was collected by the writer in 1953.

The trilobite faunas from the three localities mentioned above are identical in composition. Each contains abundant silicified specimens of all sizes that are referable to two olenellid trilobites, *Olenellus gilberti* Meek and *Paedeumias clarki* Resser, and a ptychopariid trilobite, *Onchocephalus* sp. This study is concerned only with the olenellid trilobites.

Knowledge of ontogenetic changes in olenellid trilobites up to the time of this study has been derived from examination of small suites of specimens preserved in fine-grained limestone or shale (Ford, 1877, 1878, 1881; Walcott, 1886, 1910; Kiaer, 1916; Poulsen, 1932; Riccio, 1952; Best, 1952). Lack of knowledge of a more complete ontogenetic suite for any olenellid has resulted in conflicting interpretation of available information, particularly as to the origin and development of marginal cephalic spines and primary cephalic segmentation. The purposes of this study are to describe the complete ontogenetic development of *Olenellus gilberti* Meek; to compare this with the ontogenetic development of *Paedeumias clarki* Resser; and to discuss some controversial features of the morphology of olenellid trilobites in the light of new evidence.

[1] Publication authorized by the Director, U. S. Geological Survey.

METHODS AND PROCEDURES

The silicified specimens were obtained by dissolving the enclosing blue-gray, fine-grained limestone with either dilute hydrochloric or dilute formic acid. In this instance, the results were the same with either acid. Formic acid residues of samples containing younger silicified Cambrian trilo-

bites, however, often have delicately preserved specimens that seem to be lost by treatment of the same rock with hydrochloric acid.

Residues resulting from solution of the limestone samples were decanted under water from the initial etching vessel to a fine (80 to 100 mesh) screen. The materials remaining on the screen after this step were mostly silicified trilobite fragments. The screen was then soaked in fresh water for a period of about half an hour. Following this soaking, the screen was removed and the residue was dried. The dried residue was carefully poured onto a sheet of paper and portions of this sample were scattered on a black-surface metal plate. Good specimens were then picked from the plate under a binocular microscope with a fine (00) moistened brush and placed in microfossil slides for study.

The specimens illustrated on Text-fig. 6 and 7 and Pl. 1 were chosen from many hundreds of individuals examined. Drawings were prepared by Elinor Stromberg from the writer's sketches. Photographs were prepared by N. W. Shupe.

A modified D'Arcy Thompson grid (Text-fig. 2) (Thompson, 1942, p. 1033–1039) is used to show overall changes in form of the cephalon during development. A grid of squares is superimposed on a figure of a young molt, with one of the grid intersections on the midpoint of the preoccipital segment, and one of the lines on the axial line. The comparable morphologic positions of the intersections and lines are then plotted on a figure of an adult to show which dimensional increases are proportional and which are disproportional to the rate of growth.

For statistical studies, the length of the glabella was selected as a constant to which other cephalic dimensions could be compared. A marked increase in size of the frontal lobe takes place in larger instars (Text-fig. 7) which, however, are represented by relatively few specimens. It does not appreciably effect the statistical observations.

The statistical methods used are those described by Shaw (1956). Regressions of the length of the intergenal spines, distance between the posterior tips of the palpebral lobes, distance between the intergenal spines, and breadth of the border were made on the glabellar length for 55 specimens each of *O. gilberti* and *P. clarki*. These represented all of the measurable silicified specimens of each species that were in the collections from the USGS locality 1400 at the time the statistical studies were started. The majority of these specimens have glabellar lengths of 2 mm. or less. Measurements were made with an ocular micrometer measuring 20ths or 60ths of a millimeter. The coefficient of regression (r) and the standard deviation from the regression (S_Y) were calculated for each regression. The standard error of the difference between coefficients of regression, which is a means of comparing regressions, was calculated for the regressions involving length of the intergenal spines, breadth of the border, and distance between the posterior tips of the ocular lobes.

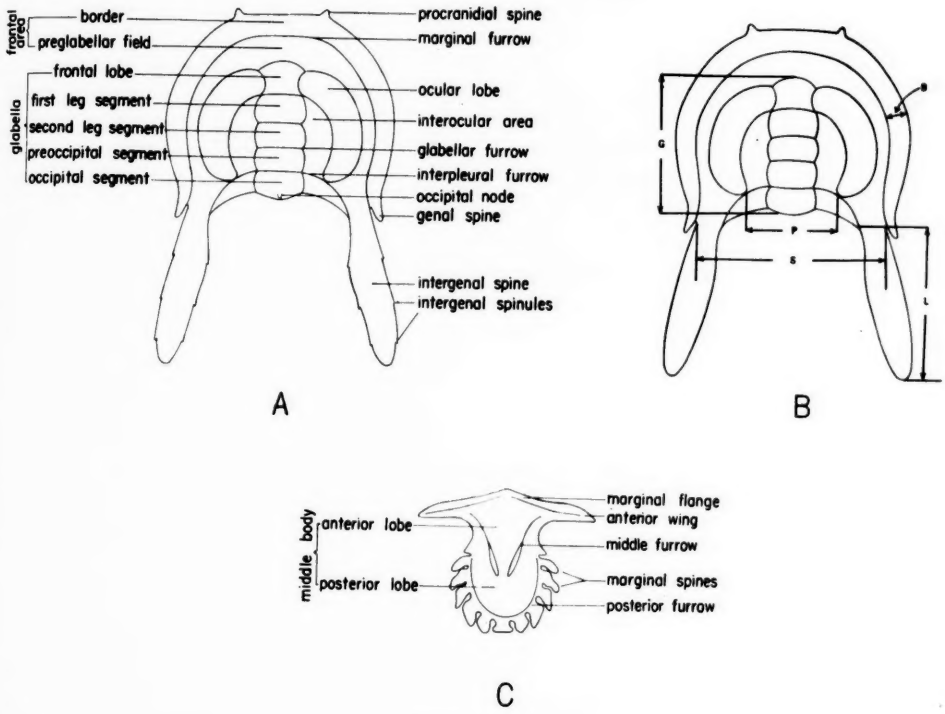
Text-fig. 1B shows the parts of the cephalon that were measured; the basic data are given in Table 1; and the results are shown on Text-fig. 3,4.

TERMINOLOGY

The terminology used here for the cephalon (Text-fig. 1A) is predominantly that discussed by Størmer (1942, p. 56–58) with slight modification (i.e., border instead of marginal rim; interpleural furrow instead of pleural furrow; and ocular lobe instead of eye lobe) to conform more closely with the standardized terminology for Cambrian trilobites proposed by Howell et al. (1947). Preglabellar field (Warburg, 1925, p. 2) is added for the region between the ocular lobes and the frontal lobe of the glabella, and the border. Hupé (1953, p. 117) has termed the area between the ocular lobes and the glabella the fixigene. The use of this term, however, also implies the presence of a facial suture separating a libragene from a fixigene. Since the presence of a facial suture in olenellid trilobites is controversial, the term *interocular area* is suggested as a neutral alternative for the fixigene of Hupé.

The intergenal spines of smaller instars of both olenellid species have three or four spinules along their inner and outer margins. These are termed here the *intergenal spinules*.

The terminology used in description of



TEXT-FIG. *1*

A,C—Terminology for describing the immature olenellid cephalon and hypostome.
B—Dimensions measured from statistical study: B—breadth of border; G—length of glabella; L—length of intergenial spines; P—distance between posterior tips of ocular lobes; S—distance between intergenal spines.

the hypostome (Text-fig. 1C) is that proposed by Warburg (1925, p. 5) and supplemented by Whittington & Evitt (1954, p. 12, 13). A new term, *marginal flange* is introduced for the ventrally deflected portion of the anterior margin.

TAXONOMY

Adults of *Olenellus gilberti* Meek and *Paedeumias clarki* Resser are so similar that specimens of both are present in the type lot of *Olenellus gilberti* Meek. The ontogenetic studies show, however, that consistent differences between the species are present, even in the earliest instars.

The most striking differences between the species are the relative degree of differentiation of the ocular lobes, glabella, and interocular areas in young specimens, and the form and direction of the intergenal spines. In young of *O. gilberti*, the ocular lobes and glabella are prominent, and the interocular areas are depressed; in young of *P. clarki*, the interocular area is not greatly depressed, and all dorsal furrows are shallow (compare Pl. 19, fig. 6,10). The intergenal spines on young of *O. gilberti* are broad, with a prominent ventral open area (Pl. 19, fig. 2, 3,12); those of *P. clarki* are narrow with only a ventral slit (Pl. 19, fig. 4). In adults, the nubs of the intergenal spines in *O. gilberti* are directed laterally; those of *P. clarki* are directed straight posteriorly (compare Pl. 19, fig. 16,20).

In addition to the directly observable differences, regressions of the length of the intergenal spines on the length of the glabella in early developmental stages, and of the breadth of the border opposite the ocular lobes and the distance between the tips of the ocular lobes on the length of the glabella on specimens of all sizes are significantly

TABLE 1.—DIMENSIONS IN MM. OF SPECIMENS OF *O. gilberti* AND *P. clarki* MEASURED FOR STATISTICAL STUDIES

Olenellus gilberti Meek					*Paedeumias clarki* Resser				
Length of Glabella (G)	Length of intergenal spines (L)	Distance between intergenal spines (S)	Distance between tips of ocular lobes (P)	Width of border opposite ocular lobes (B)	Length of Glabella (G)	Length of intergenal spines (L)	Distance between intergenal spines (S)	Distance between tips of ocular lobes (P)	Width of border opposite ocular lobes (B)
0.45	0.30	0.40	0.40	—	0.50	0.40	0.45	0.45	—
.45	.30	.40	.40	—	.55	.40	.45	.45	.050
.55	.45	.55	.55	—	.50	.30	.45	.45	—
.85	1.05	.85	.65	.125	.95	.80	1.00	.75	.100
1.40	1.50	1.75	.85	.175	2.25	1.10	3.70	1.25	.275
.70	.85	.70	.55	.100	2.55	.45	3.85	1.35	.250
2.20	1.55	4.05	1.50	.300	.50	.40	.50	.50	.050
.70	.85	.75	.55	.075	.85	.95	1.10	.65	.100
.80	1.00	.95	.65	.100	.50	.45	.50	.50	.050
.75	1.00	.75	.60	.075	.45	.35	.45	.45	—
.65	.70	.65	.55	.075	1.00	1.00	1.10	.70	.100
1.35	1.35	1.65	.80	.175	.85	.75	.80	.55	.075
1.20	1.25	1.40	.75	.175	1.40	—	2.15	.95	.150
.80	.85	.85	.60	.125	1.65	1.20	2.65	1.05	.175
.75	.90	.80	.55	.100	.50	.30	.45	.45	—
1.45	—	1.95	.90	.200	1.10	.95	1.40	.75	.100
1.85	—	3.05	1.25	.275	1.85	—	3.10	1.10	.225
1.45	1.25	2.25	.95	.225	1.00	1.00	1.20	.75	.100
.95	1.20	1.05	.70	.125	.75	—	.75	.65	.075
.60	.70	.60	.50	.075	.55	.40	.45	.50	—
3.00	.70	.45	1.70	.375	1.50	1.15	2.10	.95	.200
.50	.55	.50	.45	.050	.70	.65	.70	.65	.050
1.40	1.10	2.10	.95	.225	.65	.50	.60	.50	—
1.30	1.55	1.85	.90	.175	.80	.60	.80	.60	.075
1.10	1.20	1.35	.75	.150	1.10	—	1.25	.80	.100
.75	1.00	.70	.50	.100	2.25	.90	3.70	1.35	.225
3.15	—	5.30	1.80	.400	.70	.60	.60	.55	.050
.75	.90	.85	.60	.100	1.75	1.30	2.25	1.20	.175
1.45	1.10	1.75	.95	.200	.90	.75	1.05	.75	.100
.50	.50	.45	.40	.050	1.20	1.10	1.55	.85	.125
2.50	.50	4.50	1.60	.375	.65	.55	.55	.55	.050
.55	.70	.50	.45	.050	.70	.60	.60	.60	.050
1.20	1.40	1.50	.85	.150	.95	.75	1.00	.70	.125
.90	1.05	.95	.65	.100	.60	.40	.45	.45	—
.80	.90	.75	.55	.100	.60	.45	.45	.50	—
1.60	1.60	2.65	1.10	.250	.85	.75	1.10	.70	.125
1.50	1.45	2.35	1.10	.225	.80	.75	.80	.60	.075
1.05	1.35	1.25	.70	.150	.55	.40	.50	.50	.050
1.90	1.65	3.25	1.15	.250	.95	.90	1.05	.75	.100
1.70	—	2.15	1.00	.225	.75	.60	.60	.50	.050
.95	1.15	.90	.60	.125	.45	.35	.45	.50	—
.55	.65	.55	.45	.050	.70	.55	.55	.50	—
1.55	1.40	2.10	1.00	.225	2.65	.15	5.00	1.70	.275
1.10	1.30	1.25	.75	.150	.70	.55	.60	.60	.050
1.35	1.50	1.75	.90	.175	1.75	1.25	2.80	1.15	.225
1.90	1.70	2.25	1.15	.250	1.75	1.20	2.35	1.05	.200
2.35	2.15	4.00	1.50	.375	1.45	1.00	2.30	.95	.125
1.75	1.65	2.25	1.15	.250	.65	.55	.60	.55	.050
1.90	1.60	2.25	1.05	.250	.65	.55	.60	.60	.050
1.20	1.40	1.35	.75	.125	1.25	1.05	1.75	.95	.100
.65	.70	.60	.45	.050	.55	.35	.45	.50	—
1.00	1.25	1.30	.75	.150	.65	.50	.60	.50	.050
.55	.50	.45	.40	.050	.55	.45	.50	.50	—
3.25	.35	6.60	2.05	.500	.65	.60	.65	.60	—

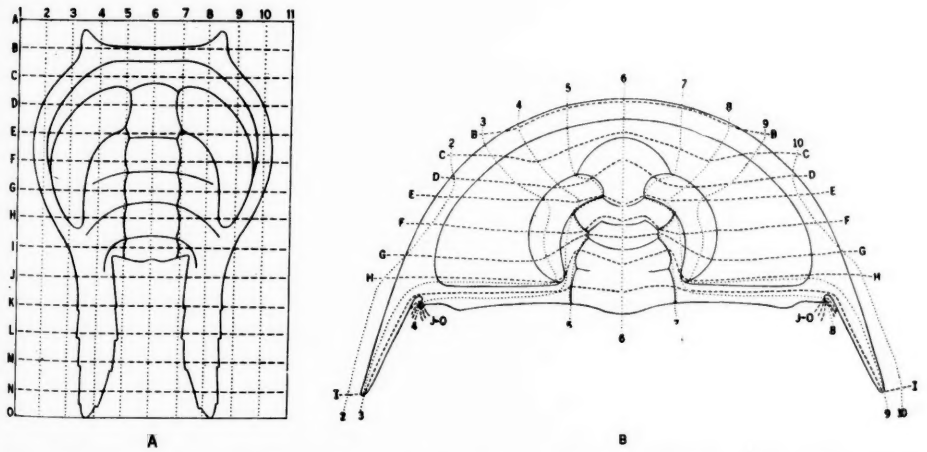
different for the two species (Text-fig. 3A, B; 4). The relative breadth of the border is considered to be a character of generic value and is the principal reason for recognizing *Paedeumias* as a genus separate from *Olenellus*. Specimens of *Paedeumias* have a consistently narrower border than those of *Olenellus* as noted by Lochman (1952, p. 95). Other characteristics that earlier workers selected to distinguish *Olenellus* from *Paedeumias* have been shown to be inadequate (Bell, 1931, p. 11; Shaw, 1955, p. 791; see below, under development of hypostome).

It has become apparent during this study that the taxonomy of olenellid trilobites is in need of a thorough reexamination. Many new species and some new genera have been proposed since Walcott's monograph on the Olenellidae (Walcott, 1910). Some authors are in disagreement on the content and limits of such genera as *Olenellus*, *Paedeumias* and *Mesonacis*. A synthesis of existing information regarding olenellid morphology, ontogeny, and startigraphic and geographic distribution that might result in a reclassification of the olenellid trilobites would be a welcome contribution to Cambrian paleontology.

OBSERVATIONS ON BIOLOGY, VARIATION, AND GROWTH

The wealth of specimens with prominent dorsal cephalic features prompted a statistical investigation of specific differences, infra-specific variation, and growth in *O. gilberti* and *P. clarki*. Preliminary to the selection of specimens for measurement, a comparison of overall changes in form during growth was made using the modified D'Arcy Thompson grid described above. This technique illustrates (Text-fig. 2) the facts that the lengths of the glabella and the cephalon, and the distance between the ocular lobes, remain nearly proportional with increasing size; that the width of the extraocular cheeks and of the glabella increases during growth; and that the length of the intergenal spines decreases during growth.

These observations may have a significant bearing on some anatomical features of the olenellid trilobites. The ocular lobes, and thus the eyes and their enervating apparatus, maintain a constant position on the head relative to the axial line. The apparent migration of the posterior tips of the ocular lobes across the pleural portion of the preoccipital segment and towards the occipital ring may actually result from the lateral expansion of the occipital ring and of the posterior margin of the cephalon. The apparent resorption of the intergenal spine during growth may also have an alternative explanation. Although the projection of the spine beyond the posterior margin of the cephalon is clearly decreased in larger molts (Text-fig. 7), the distance between the



TEXT-FIG. 2—Proportional change in dorsal cephalic features of *O. gilberti* during development. *A*—Instar IIa; *B*—Instar Ve. Intersections of vertical and horizontal lines are at the same morphologic positions on both drawings.

distal tip of the spine and the axial line measured along the preoccipital segment seems to maintain a reasonably constant ratio to the glabellar length on specimens of all sizes. Perhaps the intergenal spine is the protective covering for an organ related to the third leg that maintains a length proportional to that of the glabella throughout development. As the cephalon increases in breadth and the legs extend more nearly at right angles to the axial line, less and less of this organ and its protective cover project beyond the posterior margin of the cephalon.

The small amount of infraspecific variation is illustrated by the regressions of the breadth of the border and distance between the tips of the ocular lobes on the glabella (Text-fig. 3A,B; 4C,D). Furthermore, the differences between the regressions involving each of these characters for *O. gilberti* and *P. clarki*, although slight, are significant. The differences in breadth of the border are believed to be of generic value as stated above.

Curvilinear growth is illustrated by regressions of the distance between the intergenal spines, and of the length of the intergenal spines on the glabella (Text-fig. 3C,D; 4A,B). These figures also show that growth even of these relatively rapidly changing features is rectilinear after the first few instars. An unexpected revelation of the regression of the length of the intergenal spines on the glabellar length is the fact that the rates of development of the intergenal spines are significantly different between *O. gilberti* and *P. clarki*.

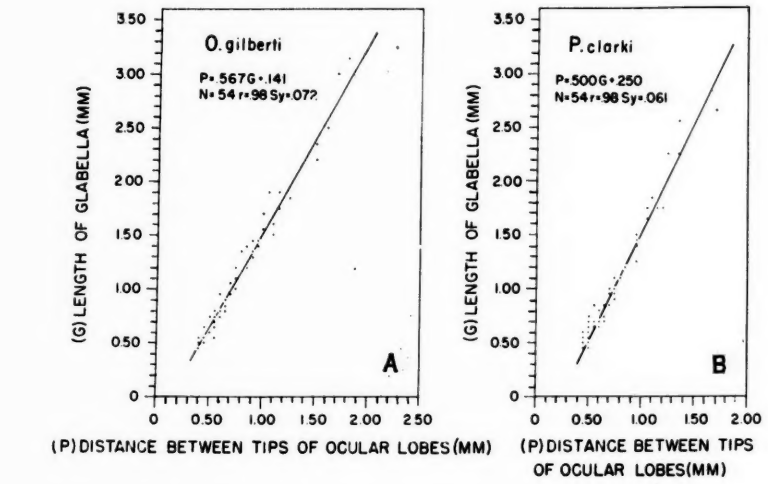
INSTARS

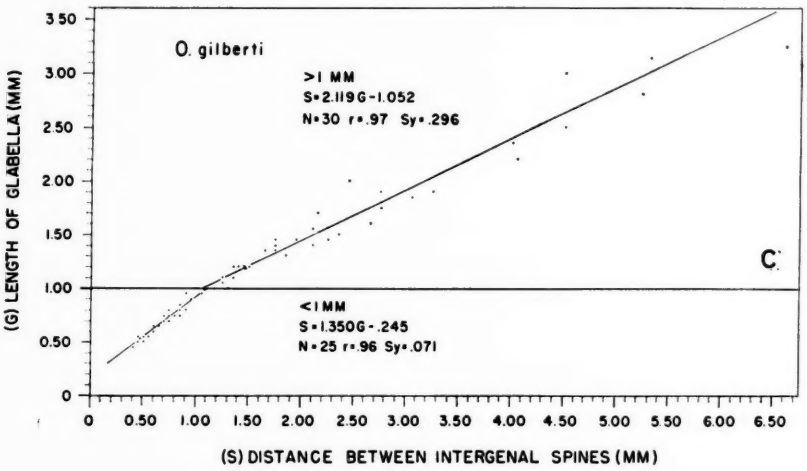
Although all arthropods are known to molt at regular intervals during their ontogeny, a sufficient number of immature specimens of a single species of trilobite has not previously been available to estimate the number of instars, and the increase in size between instars, within this group. *O. gilberti* and *P. clarki* provide the first opportunity for such a study. Each species is represented by more than 100 individuals with cephalic lengths ranging from 0.5 to slightly less than 3 mm. Larger individuals with cephalic lengths up to about 23 mm. are less common.

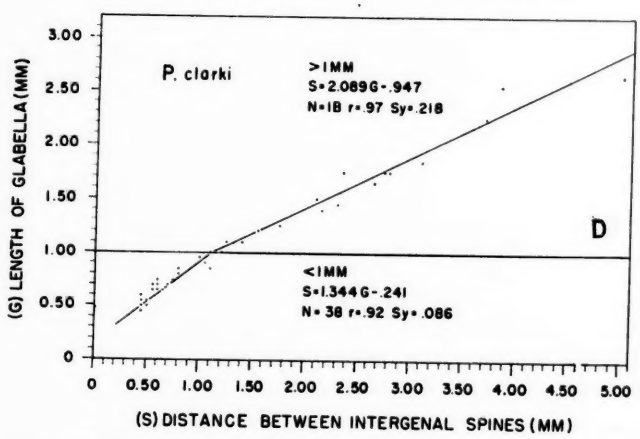
According to Dyar's law (Thompson, 1942, p. 165), linear dimensions of successive arthropod instars increase at a constant geometric rate. Thus, a growth factor can be calculated for any arthropod species that will be a measure of the percentage increase in size of linear dimensions of successive instars. In order to determine this factor for *O. gilberti* and *P. clarki*, it was necessary to find out which linear dimensions increased at a rate most nearly proportional to increases in actual size. Text-fig. 2, the D'Arcy Thompson grid, shows that dimensions along the axial line on the glabella are the least distorted from young to mature individuals.

Assuming that Dyar's law is applicable to trilobites, determination of the growth factor for *O. gilberti* and *P. clarki* was approached in three ways: (1) by determining the percentage increase in a selected linear dimension on the axial line of the cephalon for two apparently successive morphologically distinguishable forms; (2) by preparing a histogram of frequencies of occurrence of a selected linear dimension along the axial line for a large number of specimens, and calculating a growth factor that would best fit the observed peaks, assuming each peak to represent an instar; and (3) by calculating a growth factor, based on an assumption that each free thoracic segment is the result of at least one molt, and knowing the dimensions of the smallest specimen and the dimensions and number of thoracic segments of a larger specimen.

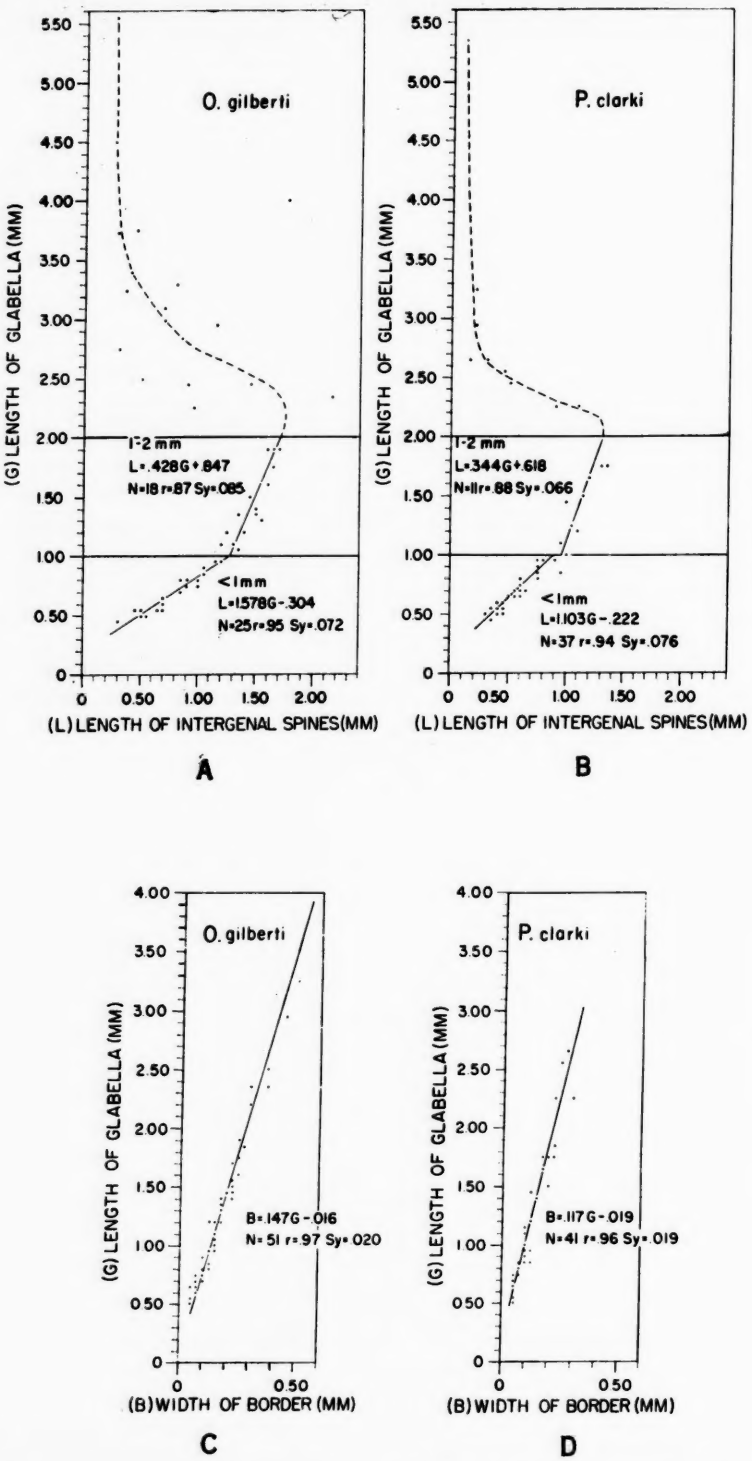
For the first determination, the smallest specimens of *O. gilberti* and *P. clarki* were used. These species are each represented by two morphologically recognizable forms, designated *a* and *b*, among the smallest specimens. There are no morphologic intergrades between these forms, and there are no forms smaller than those assigned to *a*. Measurements were made with a micrometer scale reading 60 divisions to a millimeter. The slight post-depositional deformation apparent on some larger cephala is negligible on these minute forms at the scale at which they were measured. For *O. gilberti*, the distance along the axial line from the front of the glabella to the occipital furrow was measured for three specimens of form *a* and seven specimens of form *b*. The average distances were 23.33 and 26.22







TEXT-FIG. 3—Graphic and statistical comparisons of the distance between the posterior tips of the ocular lobes (*A,B*) and the distance between the intergenal spines (*C,D*) with the length of the glabella for *O. gilberti* and *P. clarki*.



TEXT-FIG. 4—Graphic and statistical comparisons of the length of the intergenal spines (*A*,*B*) and breadth of the border (*C*,*D*) with the length of the glabella for *O. gilberti* and *P. clarki*.

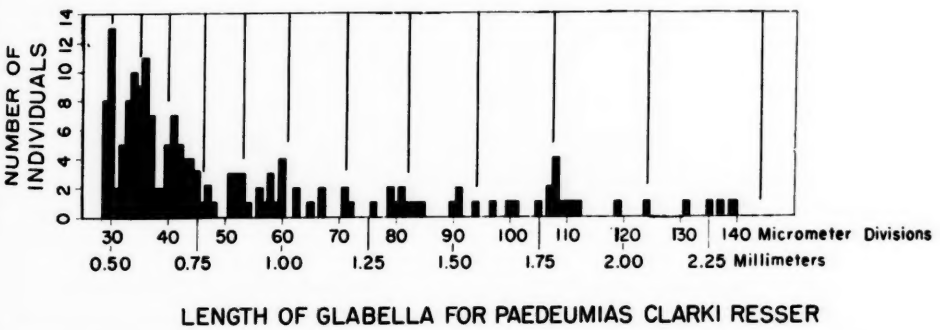
divisions respectively, indicating a growth factor of 1.12 in this dimension between *a* and *b*. For *P. clarki*, the length of the cephalon on the axial line was measured for 15 specimens of form *a* and 16 specimens of form *b*. The average distances were 33.33 and 39.00 divisions respectively, indicating a growth factor of 1.17.

For the second determination, glabellar length including the occipital ring was measured for 173 cephala of *P. clarki* at the same scale as in the previous determination. Text-fig. 5 shows histograms of the frequency of each measurement. Histograms of similar measurements of specimens of *O. gilberti* are inconclusive, perhaps due to insufficient numbers of specimens. The observations on *P. clarki* indicate three successive peaks at 30, 35, and 41 divisions, and suggested concentrations at about 51, 60, 80, and 108. A growth factor of 1.15, plotted as vertical lines on Text-fig. 5, seems to fit the observations best. The obvious lack of sufficient numbers of larger specimens makes this determination alone inconclusive. However, it is of the same order of magnitude as that obtained from the previous determination.

The third approach was applied to *O. gilberti*. Pl. 19, fig. 12 shows a specimen of *O. gilberti* that retains its thoracic segments. Examination of this specimen at high magnification shows that it has at least 10 and perhaps 12 thoracic segments and a transitory pygidium. None of the smallest specimens of *O. gilberti* show a fused protopygidium. The transitory pygidium was thus probably already free by the first instar with a preservable exoskeleton. Slightly larger specimens have two or three minute free thoracic segments, so it is a reasonable assumption that the generation of the first free thoracic segment took place between the first and second instars. If the generation of each thoracic segment required at least one molt, the specimen in figure 12 would then represent at least the 10th or 12th instar of *O. gilberti*.

If there were 10 or 12 molts between the smallest specimens and the specimen with 10–12 thoracic segments, and if Dyar's law applies, then the growth factor (K) can be calculated by measuring a common linear dimension on the smallest specimens (A) and on the large specimen bearing the thoracic segments (A′) and using the formulas: $AK^{10}=A'$, and $AK^{12}=A'$. The dimension least subject to disproportionate change during growth seems to be that along the axial line of the glabella between a line connecting the anterior margins of the ocular lobes, and the occipital furrow. This distance averages 0.39 mm. for the smallest specimens and is 1.55 mm. for the specimen bearing 10–12 thoracic segments. Using the formulas cited above, the calculated growth factors are 1.15 if the specimen had 10 free thoracic segments, and 1.12 if the specimen had 12 free thoracic segments. These figures are of the same order of magnitude as the growth factors calculated from the previous two approaches.

The average of the growth factors calculated for *O. gilberti* is 1.13 and for *P. clarki* is 1.16. The fact that different approaches


NUMBER OF INDIVIDUALS
0 2 4 6 8 10 12 14
30 40 50 60 70 80 90 100 110 120 130 140 Micrometer Divisions
0.50 0.75 1.00 1.25 1.50 1.75 2.00 2.25 Millimeters
LENGTH OF GLABELLA FOR PAEDEUMIAS CLARKI RESSER

TEXT-FIG. 5—Histograms of numbers of individuals vs. glabellar length for *P. clarki* showing evidence for distinguishing instars. Vertical lines indicate calculated mean glabellar lengths for each instar of *P. clarki* using a growth factor of 1.15.

gave reasonably consistent results indicates that 1.13 and 1.16 are probably realistic estimates of the growth factors for successive instars of *O. gilberti* and *P. clarki*.

The size ranges of specimens assigned to each of the morphologically recognizable developmental stages of *O. gilberti* are shown on Table 2. From these, the number of instars in each stage, also shown on Table 2, has been estimated. The minimum number of instars in the development of *O. gilberti* (29) was determined by calculating glabellar lengths for a series of instars having an initial glabellar length of 0.47 mm. and a growth factor of 1.13 and locating the dimension nearest the measured glabellar length of the largest cephalon in the collection, Pl. 19, fig. 19. The measured glabellar length of this specimen is nearest to the calculated glabellar length of the 29th instar of *O. gilberti*.

DEVELOPMENT OF *Olenellus gilberti*

Cephalon

The development of the cephalon of *Olenellus gilberti* Meek can be divided into five morphologic stages. The stages are designated by Roman numerals I to V. Developmental stage I contains the smallest individuals. Successive instars within each stage are indicated by letters. The first and last instars of stages I to III, and three instars each of stages IV and V are described below. Table 2 summarizes the characteristics of individual features of the cephalon through the five developmental stages.

Developmental stages Ia and Ib may correspond to the anaprotaspid and metaprotaspid periods described by Størmer (1942, p. 56) and considered by him as present in the ontogeny of all trilobites. There is no evidence in stage Ib, however, for postcephalic segments fused to the cephalon which are required if this stage is to conform to the definition given by Størmer (idem.). The possibility that the protaspid period of *O. gilberti* took place in the egg or at least before the development of a sclerotized exoskeleton should not be overlooked. Although the smallest specimens that have been observed with thoracic segments are among the larger instars of stage II, the straight posterior margin of the cephalon of stage Ia may indicate the presence of a line of articulation with thoracic segments or a transitory pygidium. The number of instars that are indicated before the instar represented by the specimen with a minimum of 10 thoracic segments, also requires early development of free thoracic segments and a transitory pygidium.

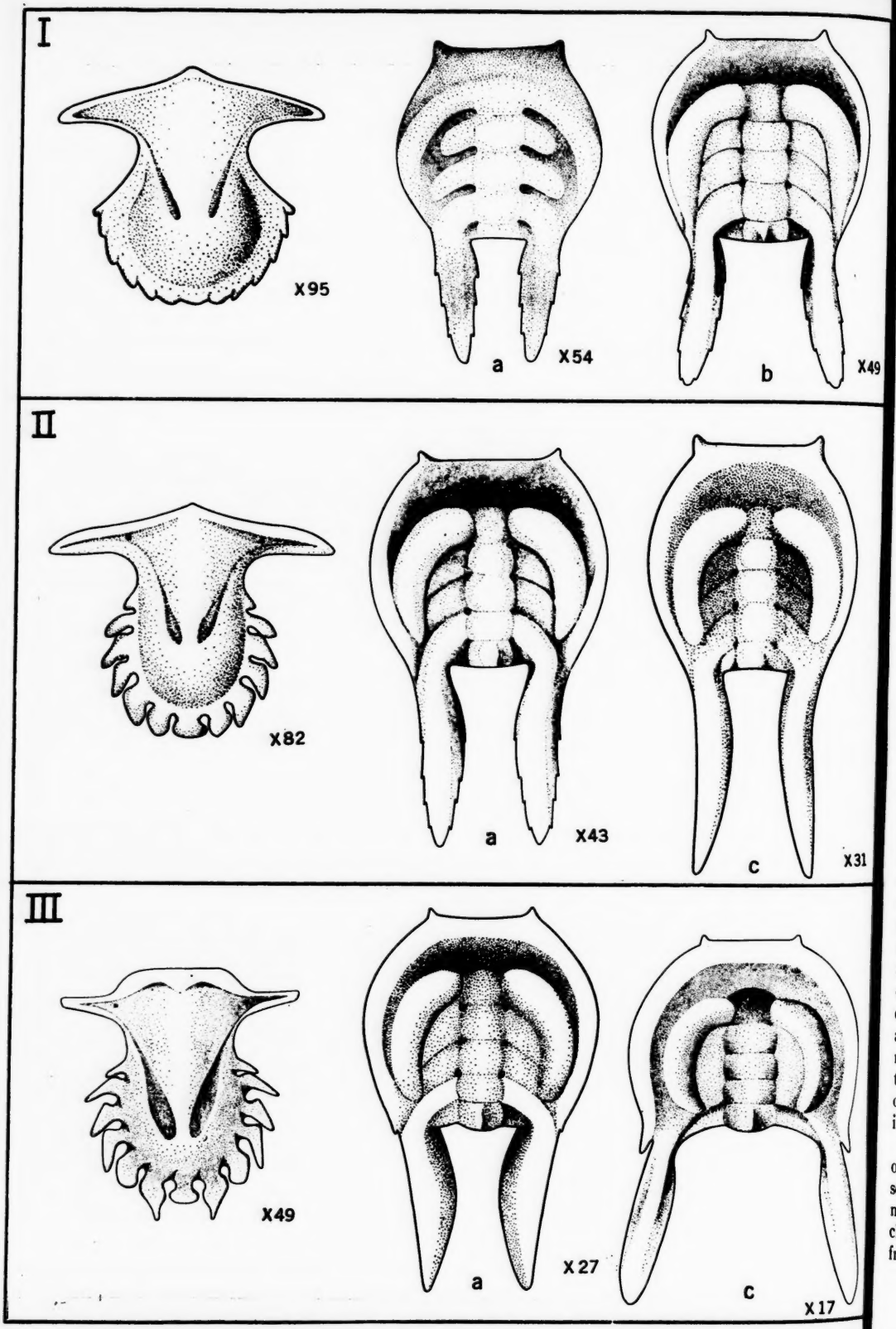
Stages I to IV, during which many profound changes take place in the morphology of the cephalon, are considered here to correspond to the meraspid period of development of non-olenellid trilobites, because of the straight posterior cephalic margin and immature form. Stage V, in which the cephalon is essentially adult in appearance, corresponds at least in part with the holaspid period of development of non-olenellid trilobites. The lack of complete specimens of earlier instars from this stage makes it impossible to demonstrate whether these have the full adult complement of thoracic segments—a necessary requirement for them to be placed in the holaspid period.

Stage I (Text-fig. 6; Pl. 19, fig. 1).—The distinguishing characteristic of specimens in this developmental stage is the absence of a distinct posterior termination of the ocular lobe. Two morphologically distinguishable instars are recognized.

Instar Ia (Text-fig. 6; Pl. 19, fig. 1): This instar has a glabellar length of about 0.50 mm. The cephalon is subcircular in outline with a slight anterior truncation between a pair of marginal procranidial spines, and a nearly straight posterior margin between prominent, posteriorly directed intergenal spines. Its greatest width is opposite the axial part of the first leg segment. The intergenal spines, nearly as long as the glabella, are depressed posteriorly at an angle of about 45 degrees to a plane passing through the cephalic margin. Each intergenal spine bears three intergenal spinules along its inner and outer margins. The ventral parts of the intergenal spines are not covered. The glabella, ocular lobes, pleural portions of the first and second leg segments, and the preoccipital segment are all at the same elevation above the frontal area. The frontal area is not differentiated into a border and a preglabellar field. Deep pits are present in the otherwise shallow dorsal furrow at the posterior margins of the frontal lobe of the glabella, the axial portions of the first and sec-

TABLE 2.—A SUMMARY OF DEVELOPMENTAL CHANGES OF INDIVIDUAL FEATURES ON THE CEPHALON OF *Olenellus gilberti* MEEK

Feature	Stage I	Stage II	Stage III	Stage IV	Stage V
Border	Undeveloped in Ia. Present only along lateral margins in Ib. Separated from intergenal spines by ocular lobes	Continuous along anterior and lateral margins by IIc. Reaches to base of integenal spines	Develops genal spines lateral to bases of intergenal spines	Continuous along all margins of cephalon by IVc.	Unchanged
Marginal furrow	Absent in Ia. Present only along lateral margins by Ib. Touches lateral margin of ocular lobes	Continuous along anterior and lateral margins by IIc. Touches lateral margins of ocular lobes, IIa–c	Touches lateral margins of ocular lobes in IIIa. Reaches cephalic margin between genal and intergenal spines by IIIc	Connects with extension of interpleural furrow between preoccipital and second leg segment by IVc.	Continuous around margins of cephalon
Preglabellar field	Undifferentiated	Undifferentiated until IIc, then present only anterior to ocular lobes	Extends laterally between ocular lobes and border by IIIc and merges with base of intergenal spines	Delineated posteriorly by marginal furrow by IVc	Unchanged
Ocular lobes	Continuous with frontal lobe of glaglabella, Ia; slightly elevated above frontal lobe in Ib; touch cephalic margin opposite first leg segment in Ia.—at base of intergenal spine in Ib. Posteror tips not defined	Prominently elevated, touch border laterally and pleural part of preoccipital segment posteriorly. Posterior tips defined	Posterior tips extend across pleural lobes of preoccipital segment by IIIc. Lateral margins touch border in IIIa, are separated from border in IIIc	Unchanged except that distance to lateral border increases	Unchanged except that distance to lateral border increases and a shallow median longitudinal furrow is developed
Frontal lobe	Continuous with ocular lobes in Ia. Depressed between ocular lobes in Ib	Unchanged	Unchanged in IIIa. Anterior margin in front of line tangent to anterior tips of ocular lobes in IIIc	More expanded anteriorly. Top at level of tops of ocular lobes by IVc	Expands around anterior tips of ocular lobes. Top slightly above tops of ocular lobes
First and second leg segments	Of equal length, interpleural furrow between pleural parts present on interocular area	Unchanged	Interpleural furrow between pleural parts disappears from interocular area by IIIc	Unchanged	First leg segment expands distally in Va, encroaches on anterior portion of second leg segment by Ve. Second leg segment also expands distally, coalesces with first leg segment by Vp
Preoccipital segment	Continuous with intergenal spines	Unchanged	Distal and proximal parts isolated by posterior tips of ocular lobes by IIIc	Unchanged	Unchanged
Occipital segment	Bears median node at posterior margin by Ib. Pleural parts subtriangular depressed below pleural portions of preoccipital segment	Unchanged	Unchanged	Unchanged	Unchanged
Procranidial spines	Present	Present	Present	Absent	Absent
Genal spines	Absent	Absent	Present, inconspicuous in IIIa; short in IIIc	Present, shorter than intergenal spines in IVa; longer than intergenal spines in IVe	Unchanged
Intergenal spines	Prominant, bear three or four pairs of intergenal spinules	Intergenal spinules disappear by IIc	Unchanged	Progressive reduced from IVa to IVe	Laterally directed nubs at inner bases of genal spines
Glabellar length	0.45 to 0.55 mm.	0.60 to 0.95 mm.	1.00 to 1.45 mm.	1.5 to 3.0 mm.	3 to at least 20 mm.
Estimated number of molts	2	3	3	5	at least 16



TEXT-FIG. 6—Development of the cephalon and hypostome of *O. gilberti*, stages I through III. Instars within each stage are indicated by letters. Total length of the hypostome and glabellar length for the cephala are held constant. Note magnifications.

ond leg segments, and the preoccipital segment. Shallow furrows connect these pits across the glabella. The frontal lobe of the glabella is scarcely differentiated from the ocular lobes. Together they form a continuous arcuate segment extending to and merging with the lateral margins of the cephalon opposite the second leg segment. The pleural portions of the first and second leg segments are well defined in the interocular area by interpleural furrows that extend laterally across the area from the pits in the dorsal furrow to the inner margins of the ocular lobe. The distal parts of the preoccipital segment extend laterally and posteriorly to form the prominent intergenal spines. The occipital segment occupies a subtriangular area between the bases of the intergenal spines. Its pleural parts are depressed in contrast to the raised pleural portions of the preceding four segments.

This instar is distinguished from the following instar principally by having the lateral margins of the ocular lobe touching the cephalic margin and by having the interspines strongly depressed posteriorly.

Instar Ib (Text-fig. 6): This instar has a glabellar length of about 0.55 mm. The intergenal spines are inclined posteriorly at an angle of about 30 degrees to the plane of the cephalic margin. Each spine bears four intergenal spinules on its inner and outer margins. The ocular lobes are slightly elevated above the frontal lobe of the glabella; their lateral margins do not reach to the cephalic margin; and their posterior tips merge with the cephalic margin adjacent to the bases of the intergenal spines. Shallow marginal furrows are developed along each side of the cephalon posterior to the procranidial spines. These furrows join the lateral margins of the ocular lobes opposite the axial portion of the first leg segment. A small node is present on the axial line at the posterior margin of the occipital segment. All other characteristics are the same as those in Ia.

The undifferentiated posterior tips of the ocular lobes and the presence of a border separating the ocular lobe from the lateral margin of the cephalon are the principal characteristics that distinguish this instar from Ia.

State II (Text-fig. 6; Pl. 19, fig. 6).—This stage includes about three instars between the appearance of clearly defined posterior tips for the ocular lobes and the appearance of genal spines. The glabellar length ranges between about 0.60 and 0.95 mm.

The distinguishing characteristics of instars in this stage are the presence of prominent, well-defined ocular lobes and of two pairs of marginal spines (procranidial and intergenal).

Instar IIa (Text-fig. 6; Pl. 19, fig. 6): In this instar, the intergenal spines are in approximately the same plane as the cephalic margin. The ocular lobes are the most prominent dorsal features on the cephalon. Their posterior tips are clearly defined, situated immediately anterior to the bases of the intergenal spines, and touching the anterior margin of the pleural lobes of the preoccipital segment. The border is differentiated from the preglabellar field only lateral to the procranidial spines. It extends posteriorly to the bases of the intergenal spines. All other characteristics are the same as in the preceding instar.

Instar IIc (Text-fig. 6): This instar differs from IIa only in the development of a shallow marginal furrow separating the preglabellar field from the border in front of the glabella and in the apparent absence of intergenal spinules.

Stage III (Text-fig. 6; Pl. 19, fig. 10–12).—This stage includes about three instars between the appearance of genal spines and the disappearance of the procranidial spines. The distinguishing characteristic of instars in this stage is the presence of three pairs of marginal cephalic spines. The glabellar length ranges from 1.00 to 1.45 mm.

Instar IIIa (Text-fig. 6; Pl. 19, fig. 2,3): In this instar, genal spines are present as minute nubs immediately outside the bases of the intergenal spines. They are directed slightly downward and can often be seen only by viewing specimens from the side or below. Other characteristics are the same as those in IIc.

Instar IIIc (Text-fig. 6; Pl. 19, fig. 11): In this instar the cephalon has a subsemicircular outline with the intergenal spines directed slightly outward rather than straight posteriorly. The anterior margin of the frontal lobe of the glabella extends in front of a line tangent to the anterior mar-

gins of the ocular lobes. The posterior tips of the ocular lobes reach to the posterior margin of the preoccipital segment isolating the distal portion of this segment, including the intergenal spine, from the proximal portion on the interocular area. The interocular area is not crossed by the interpleural furrows adjoining the second leg segment. The marginal furrow extends completely around the lateral and anterior portions of the cephalon. It cuts the posterolateral margin between the genal and intergenal spines. The preglabellar field continues laterally between the ocular lobe and the border and merges with the base of the intergenal spine. Other characteristics are the same as in IIIa.

Stage IV (Text-fig. 7; Pl. 19, fig. 12,15). —This stage includes about five instars between the disappearance of the procranidial spines and the reduction of the intergenal spines to nubs. Its distinguishing characteristic is the presence of two pairs of well-developed cephalic spines (genal and intergenal). The glabellar length ranges between 1.50 and 3.00 mm.

Instar IVa (Text-fig. 7; Pl. 19, fig. 15): Some variation is apparent in this instar. Procranidial spines are absent, but some specimens have the anterior margin of the cephalon trucated between the former positions of these spines. The anterior extension of the frontal lobe of the glabella is somewhat more prominent than in IIIc. All other characteristics are the same as in IIIc.

Instar IVc (Text-fig. 7): Specimens from this instar have the breadth of the cephalon at the posterior margin greater than the axial length. On some forms, the interpleural furrow at the posterior margin of the preoccipital segment diagonally crosses the border. This illustrates the fact that the border along the posterior margin of the cephalon in this and all larger instars is a composite of parts of the pleural lobes of the preoccipital and occipital segments. All other characteristics of this instar are the same as in IVa.

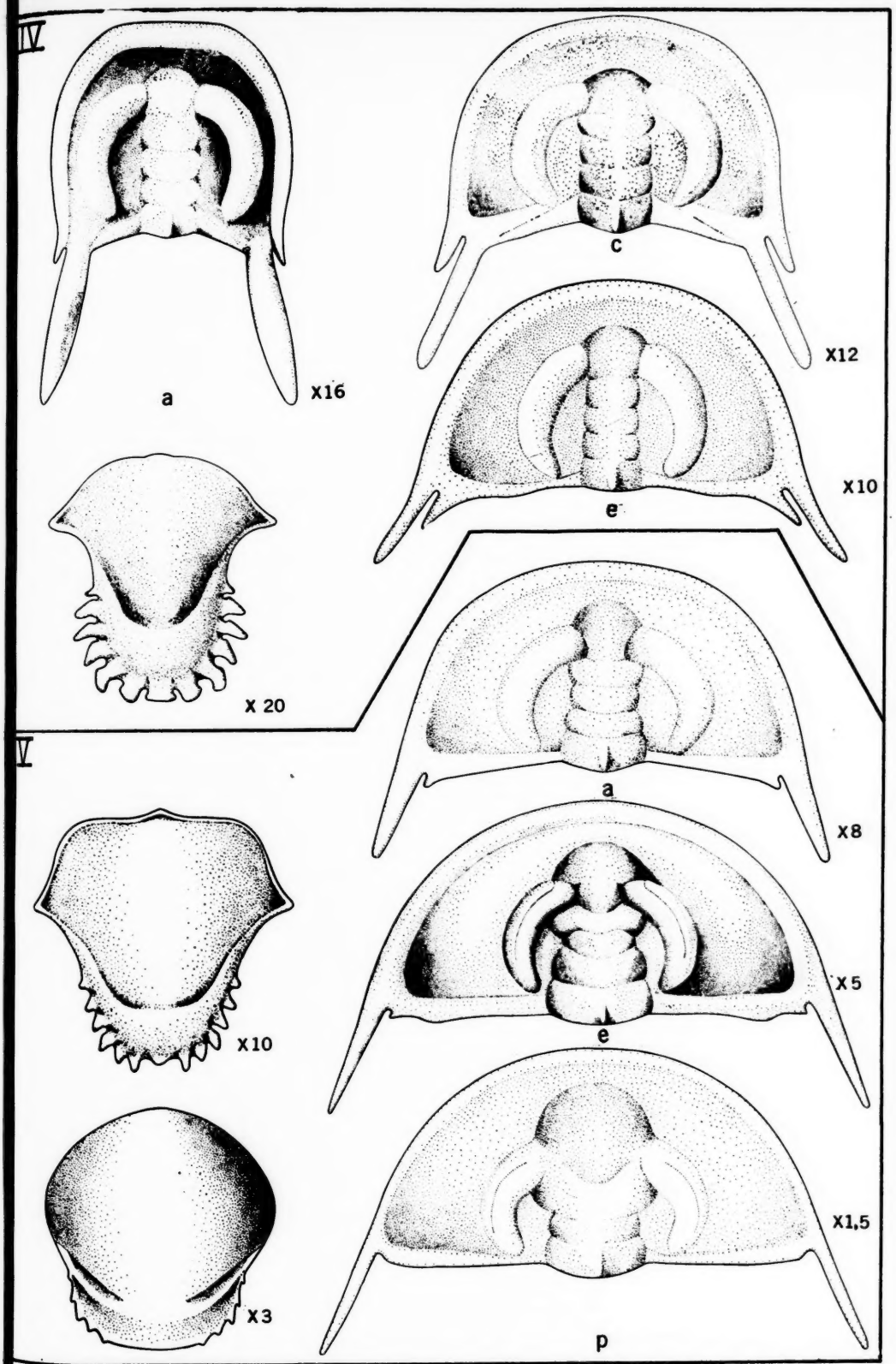
Instar IVe (Text-fig. 7): Specimens assigned to this instar show extreme variation in degree of reduction of the intergenal spines (Text-fig. 4A). The morphology is otherwise constant. The cephalon is semicircular in outline with an evenly rounded anterior margin and a nearly straight posterior margin. The frontal lobe of the glabella is elevated above the frontal area to about the same degree as the ocular lobes. A marginal furrow parallels the anterior margin to the genal angles and then curves inward parallel to the posterior margin to the posterior tips of the palpebral lobes. From this point it extends forward to join the dorsal furrow opposite the occipital furrow. The genal spines are longer than the reduced intergenal spines.

Stage V (Text-fig. 7; Pl. 19, fig. 16,19). —This stage includes all instars with the intergenal spines reduced to nubs. These instars are considered as adult. Glabellar length ranges from 3 to about 20 mm.

Instar Va (Text-fig. 7): The cephalon is semicircular in outline with its greatest width at the posterior margin. Prominent genal spines extend posteriorly from the posterolateral margin. Small, laterally directed nubs near the inner bases of the genal spines mark the remains of the intergenal spines. The glabella is prominent, elevated above the preglabellar area, and marked by four transverse furrows and a node on the axial line at the posterior margin of the occipital ring. It is narrowest at the second leg segment. Arcuate ocular lobes merge anteriorly with the expanded frontal lobe of the glabella and extend posteriorly to touch the marginal furrow near the occipital ring. A well-defined border of constant width is present along the anterior and lateral margins of the cephalon. Along the posterior margin, the border is broadest near the genal angle and tapers inward to the tips of the ocular lobes before expanding and extending to the dorsal furrow adjacent to the occipital ring.

Well-preserved uncompressed cephala of larger instars are rare. Two specimens estimated to represent the fifth and sixteenth instars of stage V are described below.

Instar Ve (Text-fig. 7; Pl. 19, fig. 16): The cephalon is semicircular in outline with a nearly straight posterior margin. Prominent, posteriorly directed genal spines are present (broken in original of Pl. 19, fig. 16). Intergenal spines are represented by laterally directed nubs near the inner bases of the genal spines. The glabella is prominent, elevated above the preglabellar area, hourglass shaped, and narrowest at the second leg segment. The frontal lobe is expanded, subovate



TEXT-FIG. 7—Development of the cephalon and hypostome of *O. gilberti*, stages IV and V. Instars within each stage are indicated by letters. Total length of the hypostome and glabellar length for the cephala are held constant. Note magnifications.

in outline, and indented at its posterolateral margins by the anterior portions of the ocular lobes. The glabellar furrow between the frontal lobe and the first leg segment is curved posteriorly along the axial line and extends laterally to the inner ends of the ocular lobes. The distal parts of the first leg segment are expanded both laterally and posteriorly, so that it and the frontal lobe seem to form parts of a subhemispherical anterior portion of the glabella that is deeply indented by the anterior parts of the ocular lobes and partly overlaps the anterolateral parts of the second leg segment. Consequently, the glabellar furrow between the first and second leg segments extends inward and forward from the glabellar margin for about one-half the distance to the axial line as a relatively deep furrow, then it bends sharply towards the axial line and extends across it as a shallow transglabellar furrow with a slight posterior curvature. The second segment is constricted along the glabellar margins by the expansion of the lateral parts of the first leg segment. The glabellar furrow between the second leg segment and the preoccipital segment is gently curved posteriorly. The occipital furrow extends only about two-thirds of the distance in from the glabellar margin to the axial line. A distinct note is present on the axial line at the posterior margin of the occipital segment. The ocular lobes are the same as those in Va except that each has a shallow median longitudinal furrow.

Instar Vp (Text-fig. 7; Pl. 19, fig. 19): Cephalon with outline like that of Ve. Glabella with frontal lobe greatly expanded. A pair of shallow indentations marks the sides of this lobe at its juncture with the anterior margins of the ocular lobes. The furrow between the frontal lobe and the first leg segment is isolated from the sides of the glabella by the ocular lobes. Its distal ends are directed straight laterally. The axial part is bowed strongly backward. The distal parts of the first and second leg segments are coalesced and expanded distally so that the furrow between the segments is represented only by a pair of pits. The enlarged subovate anterior part of the glabella, which is indented at its midlength by the anterior ends of the ocular lobes, includes the first three glabellar segments. The furrows bounding the preoccipital segment extend in from the glabellar margin only about two-thirds of the distance to the axial line. The ocular lobes are the same as those in Ve except that no distinct furrows separate the anterior portions from the frontal lobe.

Comparison with Other Immature Olenellid Trilobites

The only other known complete ontogenetic sequence of an olenellid trilobite is that of *Paedeumias clarki* Resser. This species is represented by hundreds of silicified specimens of all sizes in the collections with *O. gilberti* from the Pioche district. Although the characteristic low relief of dorsal features on the cephalon of *P. clarki* obscures some of the intersegmental furrows on young instars, the development of this species through five morphologically recognizable stages is identical to that of *O. gilberti*. Representatives of each of the stages are illustrated (Pl. 19, fig. 5,10,14,17,20) for comparison with specimens of *O. gilberti*.

Partial ontogenetic series are described or illustrated for eight North American olenellid species presently assigned to three genera [*Elliptocephala asaphoides* Emmons (Ford, 1877, p. 266–270, fig. 1–4; Walcott, 1886, pl. 17, fig. 5,6; 1910, pl. 25, fig. 1–4;11–13; Raw, 1925, p. 293–294), *Paedeumias transitans* Walcott (Walcott, 1910, pl. 25, fig. 19–22; pl. 32, fig. 1–8; Raw, 1925, p. 296–299), *Paedeumias hanseni* Poulsen (Poulsen, 1932, p. 43, pl. 11, fig. 4–9), *Paedeumias puertoblancoensis* Lochman (Lochman, 1952, pl. 19, fig. 15,16), *Olenellus gilberti* (?) Walcott (Walcott, 1910, pl. 36, fig. 11–15), *Olenellus halli* (Walcott) (Walcott, 1910, pl. 31, fig. 4–8), *Olenellus insolens* Resser (Riccio, 1952, pl. 5, fig. 1–13) and *O. bristolensis* Resser (Riccio, 1952, pl. 8, fig. 1–8)]. These studies indicate that the principal features of the ontogeny of *O. gilberti*, particularly with regard to the development of genal and intergenal spines, are common to this group of trilobites.

Individual immature specimens for three European species in two genera [*Olenellus lapworthi* Peach (Walcott, 1910, pl. 39, fig. 6), *O. reticulatus* Peach (Walcott, 1910, pl. 39, fig. 8) and *Holmia kjerulfi* Linnarsson (Kiaer, 1916, p. 66, pl. 6, fig. 1; Størmer, 1942, p. 60, text-fig. 4)] are conformable in

most observable aspects to specimens of *O. gilberti* of comparable size.

Thus, the development of *O. gilberti* can be considered as representative of most olenellid trilobites. The principal feature that does not seem to be shared by all immature olenellids is the presence of procranidial spines, although these might have been overlooked because of their small size and the imperfections of preservation of most specimens. If the spines are really absent in immature stages of some olenellid trilobites, then the presence or absence of procranidial spines might be a character of generic or suprageneric importance in the taxonomy of these trilobites.

Origin and Development of Marginal Cephalic Spines

Three pairs of marginal cephalic spines are present during early developmental stages of *O. gilberti* and *P. clarki* (Text-fig. 6): Procranidial spines at the anterolateral margins; genal spines at the posterolateral margins; and intergenal spines at the posterolateral margins in early stages of development and along the posterior margin in later stages.

Procranidial spines were first noted on an olenellid by Walcott (1910, p. 238). He described them for an immature specimen assigned to *O. gilberti* from Ptarmigan Pass, Alberta, Canada and considered them to be homologous with the prominent anterolateral marginal spines of *Olenelloides armatus* Peach from the Lower Cambrian of Scotland. He believed that these spines represented the pleural portions of an anterior marginal segment. Raw (1925, p. 306) developed a theory which he later reiterated (1936, p. 291), that procranidial spines such as those seen on the anterolateral margins of immature specimens of *O. gilberti* migrated posteriorly during development and formed the genal spines of the adult. These views are followed by Hupé (1953, p. 273). Swinnerton (in Raw, 1925, p. 323), Raymond (1928, p. 169), Stubblefield (in Raw, 1936, p. 291) and Størmer (1942, p. 66) have contested Raw's theory on the grounds of insufficient evidence.

In the complete ontogenetic series of *O. gilberti* and *P. clarki* described here, the procranidial spines maintain a constant position on the cephalic margin and they are present both before (stages I and II) and during (stage III) the early development of the genal spines. These facts show that Raw's thesis, which derives the genal spines of the adult olenellid from the procranidial spines of the young, is no longer tenable.

All authors who have considered the origin of genal spines on olenellid trilobites believe them to be the pleural extensions of a cephalic segment that lies anterior to the segment bearing the ocular lobes (antennular segment of Størmer, 1942). Raymond (1917, p. 207) and Størmer (1942, p. 121) recognize one preantennal segment and an undivided preantennal segment complex, respectively, from which to derive these spines. Walcott (1910, p. 238) recognizes two preantennal segments and considers the genal spines to originate from the inner segment. Hupé (1953, p. 273) recognizes three preantennal segments and derives the genal spine from the most anterior of these although he follows Raw in considering the adult genal spine to be developed from the procranidial spines of immature forms.

Genal spines in *O. gilberti* and *P. clarki* appear to develop from the cephalic border at the outer edges of the intergenal spines during stage III. They first appear as minute nubs directed slightly ventrally almost beneath the lateral margins of the intergenal spines and increase in length with each successive instar until an adult condition is reached. In molts IIIc and IVa (Text-fig. 6,7), the marginal furrow continues to the cephalic margin between the genal and intergenal spines. Thus, it seems that the marginal furrow along the anterior and lateral cephalic margins in olenellids may be an intersegmental furrow, and the genal spines may represent the pleural extensions of the most anterior cephalic segment. Additional speculation concerning the origin of the genal spines in olenellid trilobites is presented below in the discussion of cephalic segmentation.

Intergenal spines have been observed along the posterior margin of the cephalon in many species of olenellid trilobites. Their origin has been variously interpreted as being derived from a preantennal segment (Raymond, 1917, p. 207), from the coalesced portions of the first and second leg segments and the preoccipital segment (Ford,

1877, p. 267), from the preoccipital segment (Walcott, 1910, p. 238; Kiaer, 1916, p. 66; Stubblefield, in Raw, 1936, p. 291; Størmer, 1942, p. 123; Hupé, 1953, p. 273), or from the occipital segment (Raw, 1925, p. 232; 1936, p. 292; 1937, p. 580).

Specimens of *O. gilberti* and *P. clarki* (Text-fig. 6; Pl. 19, fig. 1,5,6,10) show clearly that the intergenal spines are the pleural portions of the preoccipital segment. Raymond's conclusion was based on a misinterpretation of the somewhat schematic drawings of *Elliptocephala asaphoides* (Emmons) described by Ford (1877). With regard to Ford's interpretation, light magnesium oxide coatings on immature specimens of *E. asaphoides* in the U. S. National Museum show shallow furrows on the interocular cheeks and indicate that the intergenal spines on this species are the pleural portions of the preoccipital segment only. Størmer (1942, p. 126–130) presents a strong argument against Raw's interpretation and in favor of the origin of the intergenal spines from the pleural portion of the preoccipital segment. His views are supported in this paper.

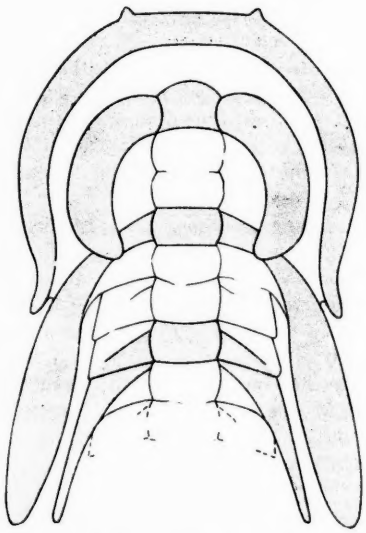
Dorsal Segmentation of the Cephalon

The number of primary dorsal segments that compose the olenellid head has been variously interpreted as six (Raymond, 1917, p. 207; Størmer, 1942, p. 123; Raw, 1925, p. 232; 1953, p. 90), seven (Walcott, 1910, p. 238) or eight (Hupé, 1953, p. 273). A modification of observations by Størmer (1942) and Raw (1953) concerning segmentation of the trilobite cephalon is presented below. It provides independent inference to support the conclusions of Hupé that the olenellid cephalon is composed of a minimum of eight primary dorsal segments.

Størmer (1942, p. 124–132) distinguishes between primary segments that make up most of the trilobite cephalon and secondary segments that make up the thorax. He theorizes that each thoracic segment is a composite of the tergal portions of two primary somites of the trilobite body. Thus, the axial part of one thoracic segment and the pleural tips of the next posterior thoracic segment he believes to be parts of the tergum of the same primary somite. The pleural parts of the occipital segment, which is the last primary segment of the cephalon, are, according to this theory, the pleural tips of the first thoracic segment; the pleural parts of the two primary somites behind the one bearing the occipital segment are the pleural tips of the second and third thoracic segments respectively; and so forth.

Raw (1953, p. 93) notes the presence of a periodicity of segment type in polynoid polychaets and in trilobites, and proposes the term merocyclism for this phenomenon. Merocyclic conditions can be expressed by regular alternations of macrosomites, which may appear as macropleural segments, and normal segments. He cites *Olenelloides armatus* Peach (Walcott, 1910, pl. 40, fig. 3) as an example of this form of merocyclism. The first two thoracic segments and the fourth and fifth thoracic segments are normal. The third and sixth thoracic segments are macropleural, thus indicating two cyclic alternations of two normal and one macropleural segment. Raw (1953, p. 86), however, is strongly opposed to the views of Størmer regarding secondary development of thoracic segmentation. Nevertheless, the principle of merocyclism can be combined with Størmer's theory of secondary segmentation of the post-cephalic segments to indicate that the olenellid cephalon may be composed of a minimum of eight primary dorsal segments.

Text-fig. 8 is a diagrammatic reconstruction of the dorsal surface of the anterior portion of a specimen in the third developmental stage of *Olenellus gilberti*. Two prominent, elongate, horseshoe-shaped segments can be seen crossing the glabella: the first includes the ocular lobes and the frontal lobe of the glabella; and the second includes the preoccipital segment and the intergenal spines. The short first and second leg segments lie between the horseshoe-shaped segments. If Størmer's theory of secondary thoracic segmentation is accepted, the occipital ring and the pleural tips of the first thoracic segment are parts of the first primary segment behind the preoccipital segment. In like manner, the axial parts of the first and second thoracic segments and the pleural tips of the second and third thoracic segments are, respectively, parts of the second and third primary segments behind the preoccipital segment. In *Olenellus gilberti*



TEXT-FIG. 8—Suggested distribution of macropleural segments (shaded) on an immature specimen (stage III) of *O. gilberti*.

the third thoracic segment is characteristically a macropleural segment (Walcott, 1910, pl. 36, fig. 9). The macropleural tip, according to Størmer, is the pleural portion of the primary segment that includes the axial ring of the second thoracic segment. Thus, beginning with the segment including the ocular lobes and the frontal lobe of the glabella, there is repeated three times a merocyclic condition of a macropleural segment followed by two normal segments.

The segments bearing the ocular lobes and the intergenal spines appear to be homologous in all olenellids, and many olenellids are characterized by having a macropleural third thoracic segment. The merocyclic condition of one macropleural and two normal segments in alternation may therefore be a feature of all olenellid trilobites.

Ontogenetic series of *O. gilberti* indicate that the genal spines originate from the border of the cephalon. Most trilobite workers consider these spines to be the pleural parts of a primary cephalic segment. Their mode of origin in *O. gilberti*, therefore, requires the presence of a macropleural segment anterior to that bearing the ocular lobes. If the merocyclic pattern discussed above is a fundamental feature of olenellid development, the macropleural segment bearing the genal spines must be separated from the segment bearing the ocular lobes by two normal segments. According to these considerations, the cephalon of *O. gilberti* consists of at least eight primary dorsal segments: 1, a macropleural segment from which the genal spines develop; 2, 3, two undifferentiated normal segments in the preglabellar area; 4, a macropleural segment including the ocular lobes and the frontal lobe of the glabella; 5,6, two normal segments, the first and second leg segments; 7, a macropleural segment including the preoccipital segment on the glabella and the intergenal spines; 8, a normal segment including the occipital ring and, by development of a secondary suture, the pleural tips of the first thoracic segment.

Hupé (1953, p. 261–264) describes two segments (*x* and *pnt*) and infers a third (p. 273, fig. 67) in front of the segment bearing the ocular lobes on olenellid trilobites. His conclusion was derived from a study of specimens in the Lower Cambrian faunas of Morocco that show the additional segments. Thus, according to his interpretation of observable features, the olenellid cephalon is composed of at least eight primary dorsal segments. The theoretical considerations presented above were arrived at independently and lend support to Hupé's conclusion.

Observational and inferential evidence now indicates that the dorsal part of the preantennal segment complex of Størmer (1942, p. 121) may be composed of at least three segments, and that the olenellid cephalon may be composed of a total of eight primary dorsal segments.

DEVELOPMENT OF THE HYPOSTOME

Hypostomes of most adult olenellid trilobites are characterized by an inflated anterior lobe of the middle body, a narrow, ventrally turned marginal flange with a short median projection, deep middle furrows and the presence of a spinose posterolateral margin. Abundant silicified olenellid hypostomes show that marked morphologic changes take place during ontogeny. Examples of hypostomes from each developmental stage are illustrated on Text-fig. 6,7 and on Pl. 19, fig. 3,7–9,13. Some specimens

in stages I, II and III have been found within cephalons (Pl. 19, fig. 3). From these it was determined that for each individual, the length of the hypostome is about equal to the length of the glabella exclusive of the occipital ring. Knowing this relationship, the assignment of larger specimens to particular developmental stages is considered to be reliable.

Riccio (1952, p. 37) attempted to distinguish between *Olenellus* and *Paedeumias* on the character of the hypostome. He illustrated a small hypostome with prominent marginal spines and a slightly expanded anterior lobe of the middle body as characteristic of *Paedeumias*. A large hypostome with a greatly inflated anterior lobe of the middle body and no obvious marginal spines was considered to be characteristic of *Olenellus*.

The hypostomes of *O. gilberti* and *P. clarki* cannot be satisfactorily distinguished in the silicified material even when found attached to a cephalon. The development of the hypostome shows that the distinctions observed by Riccio are due entirely to ontogeny and do not in any sense constitute distinctions of generic value.

Descriptions of hypostomes from each stage are given below. Table 3 summarizes the important ontogenetic changes of the hypostome.

Stage I (Text-fig. 6; Pl. 19, fig. 7).—Length about 0.41 mm. The anterior margin is turned sharply ventrally to form a narrow marginal flange. On the axial line this flange is projected into a blunt point. The anterior lobe of the middle body is subtriangular in outline and acutely pointed posteriorly. Shallow middle furrows extend inward and posteriorly nearly to the axial line at a point about two-thirds of the length of the hypostome from the anterior margin. Slender anterior wings project laterally from the anterolateral margin. At the base of each anterior wing is a depression that is expressed in the inner surface of the hypostome as a node that may be the homolog of the wing process of the cheirurid hypostome (Whittington & Evitt, 1954, p. 13). The posterior portion of the hypostome is subcircular in outline and divided by a shallow posterior furrow into the posterior lobe of the middle body and a narrow border of poorly differentiated marginal spines.

Stage II (Text-fig. 6; Pl. 19, fig. 6).—Length between 0.50 and 0.75 mm. Specimens from this stage are much like those of stage I, except that the marginal spines are well differentiated and a shallow furrow no longer separates them from the posterior lobe of the middle body. Thirteen spines are present, including six along each lateral margin of the posterior portion of the hypostome, and one posterior median spine. The distal portions of the spines are not covered on the ventral surface (Pl. 19, fig. 8). Each spine has a distinctive shape. The anteriormost pair of spines is simple; the following four pairs are foot-shaped; the sixth pair is arrowhead shaped; and the median spine is inverted-T shaped.

Specimens in this stage and stage III commonly have prominent holes in the flanks of the anterior lobe of the middle body (Pl. 19, fig. 3,8). These may represent areas of muscle attachment that were thinner than the remainder of the hypostome and were not silicified.

Stage III (Text-fig. 6; Pl. 19, fig. 3,8).—Length between 0.8 and 1.2 mm. The principal differences between hypostomes of stages II and III are somewhat greater prominence of the marginal spines and the deepening of the portions of the middle furrows nearest the axial line in stage III. The spine-bearing posterior portion of the hypostome occupies about half of the area of the hypostome.

Stage IV (Text-fig. 7; Pl. 19, fig. 13).—Length between 1.3 and 2.2 mm. Beginning in this stage, the anterior lobe of the middle body becomes broader and more convex. The marginal spines maintain their individual character but the spinose posterior portion of the hypostome occupies slightly less than one-half of the area of the hypostome rather than one-half or more as in the earlier stages.

Stage V (Text-fig. 7; Pl. 19, fig. 9). Length greater than 2.5 mm. Smaller hypostomes from this stage show an increase in breadth of the anterior body over that of specimens in stage IV. The marginal spines tend to lose their individuality and become simple. The median spine is much reduced. Larger specimens are dominated by the inflated anterior body which occupies three-fourths or more of the area of the hypostome. The anterior wings are broad and

TABLE 3.—A SUMMARY OF DEVELOPMENTAL CHANGES OF INDIVIDUAL FEATURES OF THE HYPOSTOME OF *Olenellus gilberti* MEEK

Feature	Stage I	Stage II	Stage III	Stage IV	Stage V
Anterior lobe of middle body	Narrow, outline subtriangular. Acutely pointed posteriorly. Occupies less than ⅓ area of hypostome	Form unchanged, flanks with small holes near anterior margin	Form unchanged, holes in flanks prominent. Occupies about ⅓ area of hypostome	Slightly inflated; blunted pointed posteriorly; no holes in flanks; occupies slightly more than ⅓ area of hypostome	Strongly inflated in larger specimens; occupies ⅓ or more area of hypostome
Anterior wings	Slender, straplike	Unchanged	Unchanged	Base broadens, outline subtriangular	Tips rounded, outline subsemicircular
Posterior portion	Subcircular in outline; broader than anterior lobe of middle body; occupies more than ⅓ area of hypostome	Unchanged	Outline unchanged; occupies only about ⅓ area of hypostome	Outline subquadrate; width slightly less than that of anterior lobe of middle body; occupies slightly less than ⅓ area of hypostome	Outline subsemicircular in larger specimens; occupies less than ⅓ area of hypostome
Marginal spines	Poorly differentiated	Well differentiated, each with distinct form	Unchanged	Unchanged	Lose individuality in smaller specimens; all reduced, median, anterior and posterior pairs disappear in larger specimens

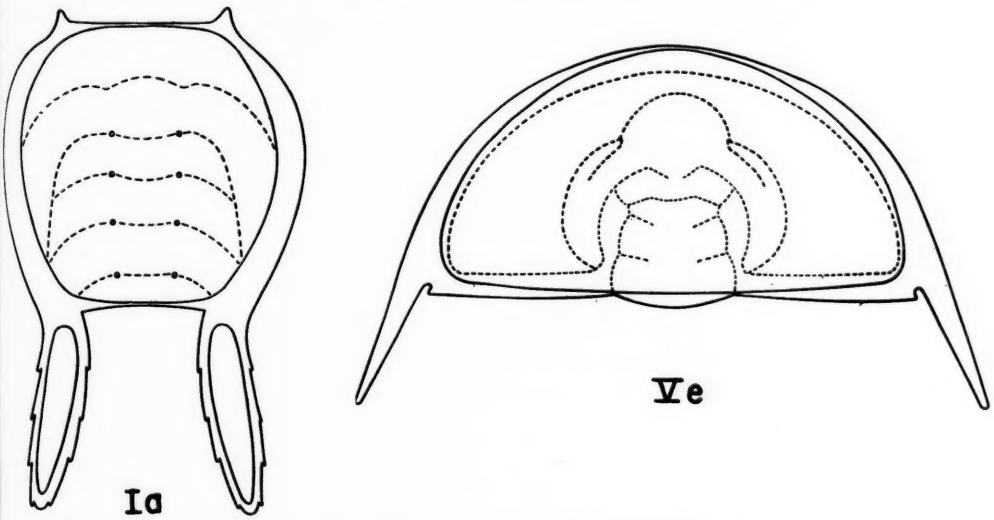
subsemicircular in outline. Marginal spines are reduced. The median spine and the most posterior and anterior pairs of lateral spines may disappear completely.

MORPHOLOGY OF THE DOUBLURE

The form of the doublure is the same for *O. gilberti* and *P. clarki* (Pl. 19, fig. 2,4). On the cephalon it is narrowest at the middle of the anterior margin and along the posterior margin near the dorsal furrows. It is widest at the posterolateral margin. Beneath the occipital ring, the doublure is widest in the axial line and tapers nearly to extinction at the dorsal furrow.

The only apparent change in the doublure from the earliest molts to the adult is in relative breadth (Text-fig. 9). In the earlier molts the doublure along most of the lateral margin is as broad or slightly broader than the border. In adult specimens, the doublure is narrower than the border.

On the hypostome, a doublure is present only along the posterior and posterolateral margins (Pl. 19, fig. 8). Instead of following the outer surface of the hypostome, it di-



TEXT-FIG. 9—Ventral views of instars Ia and Ve of *O. gilberti* showing nature of the doublure.

verges inward from this surface and forms the sides of a chamber beneath the posterior lobe of the middle body.

MORPHOLOGY OF THE ROSTRUM

The rostrum in *O. gilberti* and *P. clarki* is a slender bar that is curved in a broad semicircular arc. It is also gently curved in cross-section away from the carapace. The tips are twisted slightly so that a plane passing through the surface of the rostrum at the tip is nearly at right angles to a plane passing through the surface in the axial line. The broadest point on the rostrum is in the axial line where the posterior margin has a slight median angulation (Pl. 19, fig. 3,18). The breadth decreases regularly to the tip which is pointed in smaller specimens and broadly rounded in adult specimens. Some rostra have been found attached to the cephalon in stages I, II and III. Their tips do not seem to reach the posterolateral corners which contrasts with the conditions illustrated for *Callavia callavei* (Lapworth) (Raw, 1953, fig. 4H) and *Fallotaspis tazemmourtensis* (Hupé) (Hupé, 1953, fig. 17).

Mode of Attachment of Hypostome and Rostrum

The mode of attachment of the hypostome and rostrum may be an important means of distinguishing suprageneric groupings in olenellid trilobites. In *Olenellus* and *Paedeumias*, the hypostome seems to have been attached to the rostrum at a single point in the axial line. Walcott (1910, pl. 34, fig. 6,7) shows the hypostome of *Paedeumias transitans* Walcott connected to the rostrum by a median stalk. The kind of rostrum described in this paper, which may belong either to *O. gilberti* or *P. clarki*, has a slight median angulation along the posterior margin (Pl. 19, fig. 3,18). The associated hypostome has a prominent anterior extension of the flange. The form of the anterior margin is thus subtriangular, and the only point at which it could touch the rostrum is on the median line. The connection does not appear to have been such a pronounced stalk as Walcott shows for *P. transitans*, but most of the hypostomes and rostra that remain with cephala have been displaced slightly so that the possible presence of a fleshy attachment between the median angulation of the rostrum and the anterior marginal extension of the hypostome cannot be completely eliminated.

The condition described for *Paedeumias* and *Olenellus* is markedly different from that in *Callavia broggeri* (Walcott) (Walcott, 1910, pl. 27, fig. 2) where the hypostome appears to overlap the posterior margin of the rostrum and *Holmia kjerulfi* Linnarsson (Kiaer, 1916, pl. 7, fig. 4) and *Kjerulfia lata* Kiaer (Kiaer, 1916, p. 77, fig. 13), where the hypostome is fused to the rostrum.

CEPHALIC SUTURES

An historical summary of observations of supposed dorsal cephalic sutures in olenellid trilobites is presented by Størmer (1942, p. 136–139). He concludes that there is no direct evidence for such sutures in olenellid trilobites. Hupé (1953, p. 268–276) presents new evidence for dorsal sutures in olenellids from Morocco and reviews the arguments for such sutures in olenellid trilobites from other areas. He suggests that dorsal sutures were present in ancestral olenellids but became secondarily fused during evolution and that only vestiges of these sutures are seen on some specimens of lower Lower Cambrian olenellids.

There is no evidence at any of the known stages in the development of either *O. gilberti* or *P. clarki*. for dorsal cephalic sutures. However, these forms come from beds of latest Early Cambrian age and, thus, in accordance with Hupé's suggestion, might not be expected to retain traces of the dorsal sutures of their ancestors.

The only suture whose presence is recognized by all workers with olenellid trilobites is the marginal or perrostral suture that separates the rostrum from the doublure. Størmer (1942, p. 139; fig. 18, p. 149) speculates that this suture was at the margin of the head during the immature stages of olenellid trilobites and migrated inward to the position seen in adult olenellids because of overgrowth of the ventral portions of the cephalic margin near the genal spines. The ventral appearance of *O. gilberti* and *P. clarki* during ontogeny (Text-fig. 9) shows that this is not the case. The perrostral suture maintains a constant position within the cephalic margin throughout the development of these trilobites.

SUMMARY OF ONTOGENETIC DEVELOPMENT

Olenellus gilberti and *Paedeumias clarki* have five morphologically recognizable developmental stages in the cephalon:

I. Glabellar length about 0.45 to 0.55 mm.; characterized by lack of definition of the posterior tips of the ocular lobes and by the presence of procranidial and intergenal spines only.

II. Glabellar length about 0.60 to 0.95 mm.; characterized by well defined ocular lobes and by the presence of procranidial and intergenal spines only.

III. Glabellar length about 1.00 to 1.45 mm.; characterized by the presence of procranidial, genal, and intergenal spines.

IV. Glabellar length 1.5 to 3.0 mm.; characterized by genal and intergenal spines only; frontal lobe not greatly expanded.

V. Glabellar length greater than 3 mm.; characterized by having the intergenal spines reduced to nubs or absent and the frontal lobe of the glabella greatly expanded.

The hypostomes are essentially identical for the two species. Immature forms have slender pointed anterior wings, a narrow anterior lobe of the middle body and a relatively large posterior portion that bears 13 prominent marginal spines. Mature forms have broad rounded anterior wings, a swollen anterior lobe of the middle body and a short posterior portion with a few short marginal nubs.

The cephalic doublure in both species is broader than the border along the lateral margins in immature forms and narrower than the border along the lateral margins in mature forms. The rostrum remains essentially unchanged during development.

Instars can be recognized in both species. An increase in glabellar length by a factor of about 1.15 is indicated for successive instars. Approximately 13 instars represent the first four developmental stages.

Statistical studies show that curvilinear growth is present principally in those stages with glabellar lengths under 2 mm. Development of larger specimens for most characters appears to be rectilinear.

REFERENCES

BELL, G. K., JR., 1931, The disputed structures of the Mesonacidae and their significance: Am. Mus. Novitates, no. 475, 23 p.

BEST, R. V., 1952, Two new species of Olenellus from British Columbia: Royal Soc. Canada, Trans., vol. 46, ser. 3, sec. 4, p. 13–22, 1 pl.

FORD, S. W., 1877, On some embryonic forms of trilobites from the primordial rocks at Troy, N.Y.: Am. Jour. Sci., 3rd ser., vol. 13, p. 265–272, pl. 4.

——, 1878, Note on the development of *Olenellus asaphoides:* Am. Jour. Sci., vol. 15, p. 129–130.

——, 1881, On additional embryonic forms of trilobites from the primordial rocks of Troy, N. Y. with observations on the genera *Olenellus, Paradoxides* and *Hydrocephalus:* Am. Jour. Sci., 3rd ser., vol. 22, p. 250–259.

HOWELL, B. F., et al., 1947, Terminology for describing Cambrian trilobites: Jour. Paleont., vol. 21, p. 72–76.

HUPÉ, PIERRE, 1953, Contribution à l'étude du Cambrien inférieur et du Précambrien III de l'Anti Atlas Marocain: Serv. Geol. Maroc, Notes and Mem. 103, 402 p., 24 pl.

KIAER, JOHAN, 1916, The Lower Cambrian *Holmia* fauna at Tømten in Norway: Vidensk Selsk Christiania Skr. I, Mat.-Naturv. Kl., no. 10, 140 p., 14 pl.

LOCHMAN, CHRISTINA, 1952, in Cooper, G. A., et al., Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico: Smithsonian Misc. Coll., vol. 119, no. 1, p. 60–161, pl. 15–31.

POULSEN, CHRISTIAN, 1932, The Lower Cambrian faunas of east Greenland: Meddelelser om Grønland, Bd. 87, no. 6, 66 p., 14 pl.

RAW, FRANK, 1925, The development of *Leptoplastus salteri* and other trilobites: Geol. Soc. London, Quart. Jour., vol. 81, p. 223–431, pl. 16–18.

——, 1927, The ontogenies of trilobites and their significance: Am. Jour. Sci., 5th ser., vol. 14, p. 7–35, 131–147.

——, 1936, The Mesonacidae of Comley in Shropshire with a discussion of the classification within the family: Geol. Soc. London, Quart. Jour., vol. 92, p. 236–293, pl. 16–23.

——, 1937, Systematic position of the Olenellidae (Mesonacidae): Jour. Paleont., vol. 11, p. 575–597.

——, 1953, The external morphology of the trilobite: Jour. Paleont., vol. 27, p. 82–129.

RAYMOND, P. E., 1917, Beecher's classification of trilobites after 20 years: Am. Jour. Sci., 4th ser., vol. 43, p. 196–210.

——, 1928, Comments on "The ontogenies of trilobites and their significance" by Raw: Am. Jour. Sci., 5th ser., vol. 15, p. 168–170.

RICCIO, J. F., 1952, The Lower Cambrian Olenellidae of the southern Marble Mountains, California: So. Calif. Acad. Sci., Bull., vol. 51, pt. 2, p. 25–49, pl. 5–9.

SHAW, A. B., 1955, Paleontology of northwestern Vermont. V. The Lower Cambrian fauna: Jour. Paleont., vol. 29, p. 775–805, pl. 73–76.

——, 1956, Quantitative trilobite studies I. The statistical description of trilobites: Jour. Paleont., vol. 30, p. 1209–1244, 2 fig.

STØRMER, LEIF, 1942, Studies on trilobite morphology II: The larval development, the seg-

mentation and the sutures, and their bearing on trilobite classification: Norsk. geologisk tidsskrift, vol. 21, p. 49–164.

THOMPSON, D. W., 1942, On growth and form: The Macmillan Company, New York, 1116 p.

WALCOTT, C. D., 1886, Second contribution to the studies of the Cambrian faunas of North America: U. S. Geol. Survey Bull. 30, 369 p., 33 pl.

——, 1910, *Olenellus* and other genera of the Mesonacidae: Smithsonian Misc. Coll., vol. 57, no. 6, p. 233–422, pl. 23–44.

WARBURG, ELSA, 1925, The trilobites of the Leptaena limestone in Dalarne: Geol. Inst. Upsala, Bull., vol. 17, p. 1–446, pl. 1–11.

WHITTINGTON, H. B., & EVITT, W. R., II, 1954, Silicified Middle Ordovician trilobites: Geol. Soc. Am. Mem. 59, 137 p., 33 pl.

MANUSCRIPT RECEIVED JULY 5, 1956.

EXPLANATION OF PLATE 19

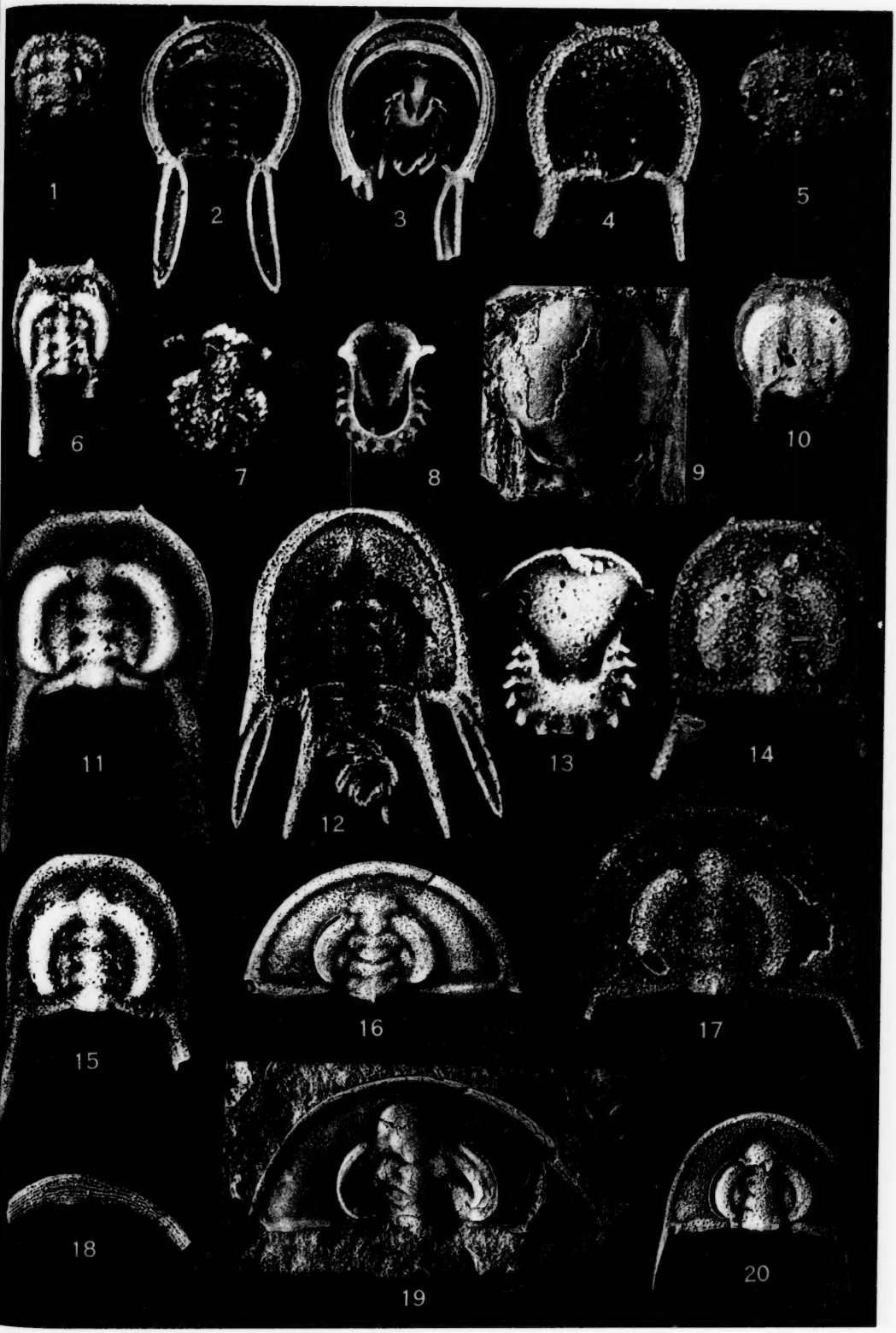
FIG. *1–3,6,11–12,15,16,19—Olenellus gilberti* Meek. *1*, dorsal view, instar Ia, ×30, USNM 126902a; *2*, ventral view, instar IIIa, showing hollow intergenal spines, ×15, USNM 126902d; *3*, ventral view, instar IIIa, showing rostrum, hypostome and several thoracic segments, ×15, USNM 126902e; *6*, dorsal view, instar IIa, ×20, USNM 126902b; *11*, dorsal view, instar IIIc, ×15, USNM 126902c; *12*, ventral view, instar IVd, showing thoracic segments, ×10, USNM 126902h; *15*, dorsal view, instar IVa, ×10, USNM 126902f; *16*, dorsal view, instar Ve, ×3, USNM 126902g; *19*, dorsal view, instar Vp, ×1, USNM 126904.

4,5,10,14,17,20—Paedeumias clarki Resser. *4*, ventral view, instar IIIa, ×15, USNM 126903b; *5*, dorsal view, instar Ib, ×30, USNM 126903a; *10*, dorsal view, instar IIb, ×20, USNM 126903c; 14, dorsal view, instar IIIc, ×15, USNM 126903d; *17*, dorsal view, instar IVc, ×10, USNM 126903e; *20*, dorsal view, instar Vc, ×4, USNM 126903f.

7–9,13—Olenellid hypostomes. *7*, external view, stage I, ×30, USNM 126905a; *8*, internal view, stage III, ×15, USNM 126905b; *9*, external view, stage V, ×3, USNM 126906; *13*, external view, stage IV, ×15, USNM 126905c.

18—Olenellid rostrum, external view, ×10, USNM 126907.

All figured specimens are from the Combined Metals bed of the Pioche shale, Pioche mining district, Lincoln County, Nevada. Fig. 1–7,9–17,19 are of specimens from USGS locality 1400–CO, on N slope of SW-directed spur, elev. about 6890, c. NE¼, NW¼, SW¼, sec. 29, T. 1 N., R. 66 E.; the specimen in fig. 9 is from USGS locality 1392–CO, E side of Pioche-Caselton rd., about 1 mile S of Pioche, c. NE¼, sec. 27, T. 1 N., R. 67 E.; the specimen in fig. 18 is from USGS locality 1399-CO, on E side of Pioche Hills, about 1 mile NW of Pioche, near c. sec. 16, T. 1 N., R. 67 E., (collected by G. A. Cooper and H. B. Whittington, 1954).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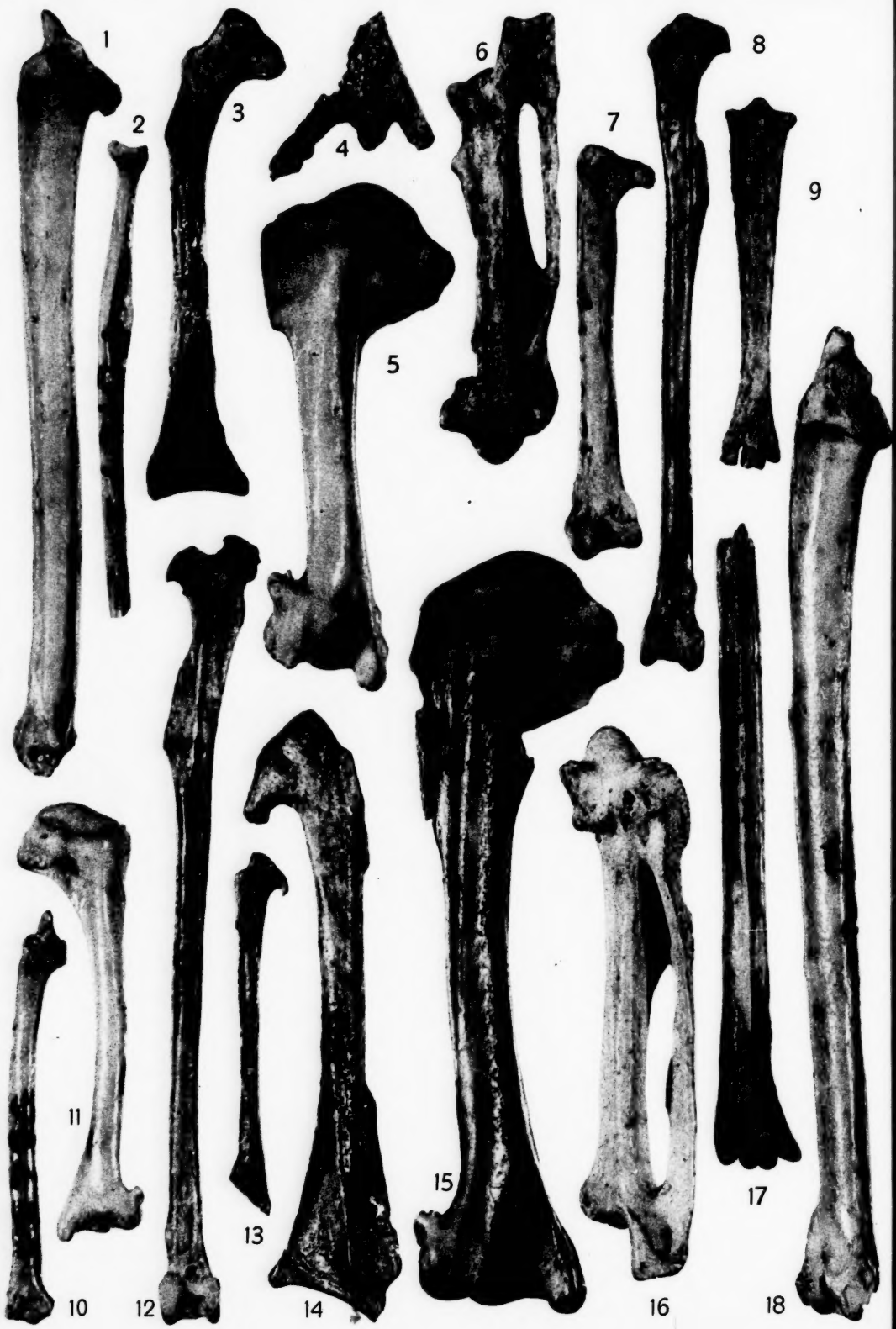
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JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 1, P. 129–138, PL. 20, 1 TEXT-FIG., JANUARY 1957

NEW PASSERINE BIRDS FROM THE PLEISTOCENE OF REDDICK, FLORIDA

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ABSTRACT—From a deposit formed in a cave during the Illinoian stage of the Pleistocene 52 species of birds are reported. The following passerines are described as new: *Tachycineta speleodytes*, *Protocitta dixi* (new genus, Corvidae), *Cistothorus brevis*, and *Pandanaris floridana*. In the absence of osteological characters *Iridoprocne* Coues is combined with *Tachycineta* Cabanis, and *Telmatodytes* Cabanis is included in *Cistothorus* Cabanis. Nine living species are added to the fossil record. Most of the birds from the deposit still occur in Florida today. Of the 11 extinct species, one is of uncertain affinities, five belong to a southwestern or Sonoran fauna, and five represent a boreal fauna. Parallel faunal origins exist among the mammals. The climate at Reddick during the Illinoian stage is believed to have been at least as cool as that of Virginia today.

INTRODUCTION

THE largest fossil vertebrate fauna yet discovered in Florida occurs in a Pleistocene deposit near Reddick, where during the last few years 4000 specimens of birds have been collected. Reptiles and amphibians are also abundant, and remains of mammals outnumber those of the birds at a ratio of about 175 to one.

As much of the material is still unstudied, relatively little has been published on the Reddick locality. Gut (1939, p. 54) listed 19 species of mammals, but according to recent information supplied by him the mammalian list now stands at 50 species, of which half represent extinct genera or species. Pleistocene indicators among the mammals include a short-faced bear (*Arctodus floridanus*), a dire wolf (*Canis ayersi*), lemming (*Synaptomys australis*), glyptodont (*Boreostracon floridanus*), ground sloth (*Paramylodon* sp.), armadillos (*Dasypus bellus* and *Holmesina septentrionalis*), mammoth (*Mammuthus* sp.), horse (*Equus* sp.), tapir (*Tapirus veroensis*), peccaries (*Platygonus* sp. and *Mylohyus* sp.), and camel (*Tanupolama mirifica*).

Auffenberg (1955, p. 135) published on a lizard from Reddick, and Goin & Auffenberg (1955, p. 500) on a salamander. The herpetological material currently at hand numbers about 50 species.

The only birds hitherto reported are three rails (Brodkorb, 1952, p. 80; 1954, p. 103). In the present paper the list of birds is increased to 52 species, and four new species of passerines are described. The types are retained in the Brodkorb collection at the University of Florida.

STRATIGRAPHY

The fossil locality lies in a pit of the Dixie Lime Products Company, one mile southeast of Reddick, Marion County, Florida, in the SW corner, NW ¼, sec. 14, T. 13 S., R. 21 E. The surface elevation here is 95 feet above mean sea level.

The superficial layer (Bed 1) is composed of Newberry sand (Matson & Sanford, 1913,

EXPLANATION OF PLATE 20

FIG. *1–9—Tachycineta speleodytes*, n. sp. *1*, ulna, 1271; *2*, radius, 1272; *3*, coracoid, 1088; *4*, rostrum, 423; *5*, holotype humerus, 1270; *6*, carpometacarpus, 431; *7*, femur, 1537; *8*, tibiotarus, 1544; *9*, tarsometatarsus, 1539. *1–3*, ×5; *4–9*, ×4.75.

10–13—Cistothorus brevis, n. sp. *10*, ulna, 790; *11*, holotype humerus, 788; *12*, tibiotarsus, 473; *13*, coracoid, 476. All ×2.75.

14–18—Protocitta dixi, n. gen., n. sp. *14*, coracoid, 1372; *15*, holotype humerus, 428; *16*, carpometacarpus, 1030; *17*, tarsometatarsus, 1245; *18*, ulna, 425. All ×5.5.

p. 32). This formation consists of orange brown (reddish brown to yellowish brown) clayey sand, weathering grayish buff. The unit is massive and has a thickness of 21 feet. It represents the Wicomico marine terrace of the Sangamon interglacial stage of the Pleistocene (Cooke, 1945, p. 281; MacNeil, 1950, p. 102). The Wicomico terrace occupies a large part of peninsular Florida between the 70 and 100 foot contours. The scarp of the Wicomico shore lies a few yards west of the present site.

Bed 2 is largely composed of stratified clayey sand, buff in color, and in places grading to buff sandy clay or brown clay. It has an average thickness of 14 feet. Locally the upper four feet of the unit consists of stratified bluish gray clayey sand, alternating with yellow clayey sand. The non-marine origin of Bed 2 is attested by the presence of land shells and the remains of frogs and salamanders.

A non-marine Pleistocene bed underlying the Wicomico terrace must represent a glacial stage, since this area was inundated by the sea during all interglacial stages previous to Sangamon time. Therefore, the blue and yellow stratified sand forming the top of Bed 2 is thought to reflect the rising water table accompanying the encroachment of the sea near the close of the Illinoian glacial stage. It is believed to be the equivalent of thick deposits of blue and yellow fresh water clay which occur at comparable elevations below the Wicomico terrace over much of Alachua County to the north.

The main bone bed occurs in a locality in the buff clayey sand of Bed 2. It has a depth of 2 feet, an estimated width of 10 feet, and extends in a southeasterly direction for a distance of about 180 feet. A section through the central portion of the bone bed was destroyed by mining operations about five years ago, so that only the two end portions remain. The matrix here contains numerous fragments of limestone, interpreted as indicating the collapse of the roof of a cave. The abundance of bones of small vertebrates at this site is almost beyond comprehension. Remains of small rodents, insectivores, and bats are especially common. Bones occur in lesser numbers in a zone extending about eight feet above the top of the main bone bed. Remains of larger vertebrates are more frequent high in the section and near what is thought to have been the mouth of the cave.

A second site occurs 260 feet southwest of the main bone bed. The matrix here is buff sandy clay, and likewise contains limestone fragments. The fossils are much less concentrated and include a higher proportion of large forms and snakes.

Infrequent vertebrate remains occur in various other parts of the mine in the lower 10 feet of Bed 2.

Bed 3 is composed of friable white limestone of the Ocala formation of the Upper Eocene. Its surface is pitted and irregular, and it outcrops to the west well above the 100 foot contour. This limestone is subject to extensive solution by ground water, resulting in numerous sinks and caves.

SYSTEMATIC PALEONTOLOGY

Order PASSERIFORMES

Family HIRUNDINIDAE

Genus TACHYCINETA Cabanis

Diagnosis.—Humerus with (1) pneumatic fossa with a tiny foramen, as in *Hirundo*, *Riparia*, *Petrochelidon*, and *Progne* (foramen occupying nearly entire fossa in *Stelgidopteryx*); (2) angle formed by deltoid crest and external tuberosity 120 degrees or less, as in *Hirundo*, *Riparia*, *Petrochelidon*, and *Progne* (130 degrees or more in *Stelgidopteryx*); (3) base of median crest shorter than portion joining internal tuberosity, as in *Hirundo*, *Riparia*, *Petrochelidon*, and *Progne* (base longer than internal tuberosity portion in *Stelgidopteryx*); (4) distal border of median crest produced at an angle away from internal tuberosity, as in *Riparia* (gently curved in *Hirundo*, *Petrochelidon*, *Stelgidopteryx*, and *Progne*); (5) base of internal tuberosity excavated by pneumatic fossa, as in *Stelgidopteryx* (unexcavated in *Hirundo*, *Riparia*, *Petrochelidon*, and *Progne*); (6) head moderately excavated by medial branch of M. triceps, as in *Progne* (deeply excavated in *Hirundo*; shallowly excavated in *Riparia*, *Petrochelidon*, and *Stelgidopteryx*).

Carpometacarpus in medial view with (1) metacarpal three relatively straight, as in *Hirundo*, *Stelgidopteryx*, and *Progne* (bowed in *Petrochelidon*); (2) intermetacarpal tuberosity exposed below shaft of metacarpal

three, as in *Stelgidopteryx* and *Progne* (hidden in *Hirundo* and *Petrochelidon*); (3) facet for digit three somewhat notched, with lower end the longer, as in *Hirundo* (obliquely truncate, with lower end longer in *Petrochelidon* and *Progne*; notched with upper end longer in *Stelgidopteryx*); (4) distal symphysis slightly excavated, as in *Hirundo*, *Petrochelidon*, and *Progne* (deeply excavated in *Steligidopteryx*). The carpometacarpus of *Riparia* is unavailable.

Coracoid with (1) head strongly deflected medially, as in *Hirundo* (less deflected in *Riparia*, *Petrochelidon*, *Stelgidopteryx*, and *Progne*); (2) edge of sternocoracoidal process jagged, as in *Hirundo*, *Riparia*, and *Petrochelidon* (entire in *Stelgidopteryx* and *Progne*).

In osteological characters *Iridoprocne* Coues (1878, p. 412) agrees with *Tachycineta* Cabanis (1850, p. 48) and is here included under the older name.

Tachycineta speleodytes, n. sp.
Pl. 20, fig. 1–9

Holotype.—Complete left humerus (1270), with associated left ulna (1271) and proximal portion of left radius (1272). From Illinoian stage of Pleistocene at Dixie Lime Products Company mine, one mile southeast of Reddick, Marion County, Florida. Collected by Pierce Brodkorb, January 1, 1955.

Paratypes.—Sixteen complete humeri, eight lefts (406, 426, 554, 708, 795, 827, 1231, 1232) and eight rights (405, 456, 553, 670, 744, 828, 1066, 1178).

Diagnosis.—Similar in size to living *Tachycineta bicolor* (Linnaeus), but humerus with (1) deltoid crest shorter and produced proximally, so that caput humeri, external tuberosity, and deltoid crest make a line almost at a right angle to shaft; (2) internal tuberosity longer and less hooked distally; (3) capital groove shorter and less overhung by head; (4) bicipital crest more contracted proximally.

Referred Material.—Humerus: four lefts (411, 588, 748, 754) and five rights (822, 883, 996, 1073, 1124). Twenty-four juvenile humeri, 16 lefts (217, 218, 219, 221, 408, 409, 410, 412, 427, 555, 576, 691, 749, 942, 991, 1240) and 18 rights (220, 407, 581, 709, 796, 797, 847, 892, 943, 992, 993, 1072, 1090, 1100, 1101, 1129, 1133, 1319). Measurements of adult humeri are given in Table 1.

Rostrum: 423. Slightly wider and apparently shorter than in *T. bicolor*. Width at zygoma, 4.0; width of nasal bridge, 0.7 mm.

Coracoid: 214, 216, 413, 987, 1088, 1528 (lefts); 213, 215, 1529 (rights). Only 1088 is adult. Differs from *T. bicolor* in lacking hook on brachial tuberosity. Length, 15.4–16.5; width through glenoid facet, 1.6–1.8; width of shaft, 1.0–1.2 mm.

Ulna: 414, 415, 416, 419, 420, 432, 671, 916, 928, 1271 (lefts); 417, 421, 433, 582, 918, 926, 939, 994, 995 (rights). External cotyla less hooked than in *T. bicolor*. Length (5 adults), 23.5–24.4 mm.

Carpometacarpus: 422, 431, 1089 (lefts); 222, 1099, 1112, 1538, 1542 (rights). Median tubercle along tendinal groove of metacarpal two more distal than in *T. bicolor*. Length (5 adults), 14.7–15.0 mm.

Femur: 1537, left, subadult. Posterior face more excavated than in *T. bicolor*. Length, 13.9 mm.

Tibiotarsus: 436, 1074, 1087, 1536, 1544 (lefts). Compared with *T. bicolor* fibular crest longer, more rotated to rear, and with proximal portion gently merging with shaft instead of dropping off abruptly. Length, 21.1–21.8; distal width, 2.2–2.3; width of shaft, 1.0 mm. (3 adults).

Tarsometatarsus: 434, 435, 1539, 1540, all juvenile rights. Length (1), 12.5 mm.

Table 1.—Measurements (mm.) of Adult Humeri of *Tachycineta speleodytes*

Measurement	No.	Range	Mean	Standard Deviation
Length	20	14.5–15.6	14.99 ± .07	0.33 ± .05
Proximal width	11	6.3– 6.7	6.50 ± .04	0.13 ± .03
Distal width	20	4.3– 4.7	4.46 ± .05	0.12 ± .02
Width of shaft	25	1.7– 2.1	1.86 ± .02	0.11 ± .01
Length of deltoid crest	17	3.1– 3.6	3.33 ± .03	0.12 ± .02

According to Lambrecht (1933, pp. 636, 775), *Hirundo fossilis* Giebel is identical with the living *Hirundo rustica* Linnaeus. If this is correct, then *Tachycineta speleodytes* is the first fossil species of swallow.

Family CORVIDAE
Genus PROTOCITTA, n. gen.
Type species: *Protocitta dixi*, n. sp.

Diagnosis.—Humerus resembles that of *Calocitta* Gray, of Mexico and Central America, in extent and general shape of pneumatic fossa; length of medial bar; development of internal tuberosity, bicipital crest, and external condyle; extent of groove between condyles; and shape and size of attachment for anterior articular ligament.

Differs from *Calocitta* as follows: In ventral view, (1) anconal surface of internal tuberosity rounded, with proximal portion more bulging, distal portion convex instead of concave; (2) juncture of medial bar with internal tuberosity less angular. In distal view, (3) pneumatic fossa rhombodial instead of elliptical, extending less toward medial portion of bone, and with its borders more compressed and angular; (4) medial bar at an angle of about 60 degrees to palmar side of pneumatic fossa instead of about 45 degrees; (5) median portion of medial bar more curved toward palmar surface. In palmar view, (6) ectepicondylar process with its base more excavated distally.

Less closely related to *Psilorhinus* Rüppell, of Mexico and Central America, from which the humerus differs as follows: In ventral view, (1) medial bar shorter, and its juncture with internal tuberosity more angular; (2) medial bar nearly at a right angle to shaft, instead of at about 45 degrees; (3) pneumatic fossa less extensive proximally, bending at nearly a right angle at base of internal tuberosity to occupy about the lower half of the latter, instead of bending at 45 degrees and occupying the lower two-thirds of the internal tuberosity. In distal view, (4) medial bar slightly curved in middle toward palmar surface, instead of lying nearly straight; (5) angle from medial bar to shaft about 60 degrees, instead of 45; (6) angles formed from medial bar to internal tuberosity more pronounced; (7) internal tuberosity less produced toward caput humeri and less overhanging capital groove. In palmar view, (8) external condyle less produced distally; (9) groove between internal and external condyles wider and shallower.

More distantly related to *Pica* Brisson, of the Holarctic region, differing as follows: In ventral view, (1) angle formed by medial bar and internal tuberosity much less prominent; (2) proximal portion of internal tuberosity more bulging, distal portion more nearly square. In distal view, (3) angle of medial bar to palmar side of pneumatic fossa about 60 degrees, instead of about 30 degrees; (4) medial bar curving in middle toward palmar surface, instead of nearly straight; (5) distal inner corner of pneumatic fossa less excavated; (6) internal tuberosity extending less toward head and thus less overhanging capital groove. In palmar view (7) proximal portion of bone wider, with bicipital crest better developed; (8) external condyle less produced distally; (9) attachment for anterior articular ligament considerably larger and extending obliquely proximad, instead of having its upper medial end truncate toward internal condyle; (10) groove between condyles wider and shallower; (11) ectepicondylar process extending from shaft at a great angle, with its base more excavated both proximally and distally.

PROTOCITTA DIXI, n. sp.
Pl. 20, fig. 14–18

Holotype.—Left humerus, nearly complete (428). From Illinoian stage of Pleistocene at Dixie Lime Products Company mine, one mile southeast of Reddick, Marion County, Florida. Collected by E. J. Moughton, Jr., in 1937.

Paratypes.—Distal portions of two left and one right humeri (351, 832, 839).

Diagnosis.—Humerus about the same size as in *Calocitta formosa*, *Pica pica*, and *Pica nuttallii;* distal width greater than in *Pica;* proximal width greater than in *Calocitta formosa.*

Length, 43.2; proximal width, 13.1; width of shaft (3), 4.1; distal width (4), 10.6–11.3; length of external condyle (3), 4.3–4.7; height of internal condyle (4), 2.8–3.2 mm.

Humerus smaller than in *Calocitta col-*

liei, *Psilorhinus morio*, and *Psilorhinus mexicanus*, much larger than in any other jay examined.

Referred Material.—Coracoid: two lefts, 968 and 1372. Differs from both *Calocitta* and *Psilorhinus* in having (1) head more pointed, through greater excavation of upper end of coraco-humeral surface; (2) pneumatic fossa on inner face of base of hook of brachial tuberosity elongated (rounded and nearly closed in *Calocitta*, large and wide in *Psilorhinus*). Length 31.5–32.9; head to procoracoid, 10.4; width of sternal facet, 8.3; width of shaft, 2.3–2.5 mm.

Ulna: left complete, 425. Resembles ulna of *Calocitta formosa*, but (1) tricipital groove more pronounced; (2) margin between olecranon and external cotyla, on anconal surface, excavated lateral to tricipital groove, instead of straight; (3) shaft stouter. In the first two characters the ulna resembles that of *Psilorhinus*, from which the new species differs in having the shaft stouter and the internal condyle smaller. Length, 55.9; proximal width, 7.6; maximum distal depth, 6.5; width of shaft, 3.4 mm.

Carpometacarpus: right complete, 1030. Slightly longer than in *Psilorhinus mexicanus*, much longer than in *Calocitta formosa*. Differs from both those species in having (1) distal end of metacarpal three wide and truncate, instead of coming to a rounded point; (2) inner face of metacarpal three with concave distal portion separated by a raised convex area from intermetacarpal space; (3) tendinal groove on dorsal surface of metacarpal two with an ossified bridge at its proximal end. Agrees with *Calocitta* and differs from *Psilorhinus* in having only slightly developed the bar separating pit at base of external trochlea from intermetacarpal space. Agrees with *Psilorhinus* and differs from *Calocitta* in lacking a pit at inner anterior base of process of metacarpal one. Length, 31.5; length to metacarpal two, 28.4; distal height through metacarpal two, 7.0 mm.

Tarsometatarsus: distal portions of two lefts (833 and 1245) and two rights (786, 881). Differs from *Calocitta* and *Psilorhinus* in having (1) trochleae slightly more separated; (2) facet for metatarsal one lower on shaft. Distal width (3), 5.0–5.2; least width of shaft (3), 2.4–2.5; height of proximal end of foramen above trochlea four on distal face (3), 3.8–4.5 mm. The tarsometatarsus indicates a long- and slender-legged jay with feet adapted for locomotion as in a magpie (*Pica*), nutcracker (*Nucifraga*) or chough (*Pyrrhocorax*).

This species is the first fossil jay described.

Family TROGLODYTIDAE
Genus CISTOTHORUS Cabanis

Diagnosis.—Compared with other genera of wrens examined (*Salpinctes*, *Campylorhynchus*, *Thryothorus*, *Thryomanes*, and *Troglodytes*), the humerus differs in having (1) deltoid crest short, weak, and with a notch near distal end; (2) shaft narrow and more bowed; (3) pneumatic fossae one and two shallower; (4) ligamental furrow shallower; (5) proximal and distal ends narrower.

As *Telmatodytes* Cabanis (1850, p. 78, note) does not differ from *Cistothorus* Cabanis (1850, p. 77, note) in osteological characters, the two are combined under the name with page priority.

CISTOTHORUS BREVIS, n. sp.
Pl. 20, fig. 10–13

Holotype.—Complete right humerus (788). From Illinoian stage of Pleistocene at Dixie Lime Products Company mine, one mile southeast of Reddick, Marion County, Florida. Collected by Faye Jean Gut, March 8, 1953.

Paratypes.—Complete left (437), four left distal (474, 716, 792, 1627), right proximal (715), and right distal humeri (1530).

Diagnosis.—Humerus resembles that of living *Cistothorus stellaris* (Naumann), but differs in having (1) length less; (2) entepicondyle slightly narrower; (3) internal tuberosity better developed.

Differs from living *Cistothorus palustris* (Wilson) in having (1) length less; (2) entepicondyle slightly narrower; (3) caput humeri narrower and more pointed; (4) internal tuberosity less developed and making a lesser angle with anconal plane; (5) distal end slightly narrower.

Length (2), 12.2–12.3; proximal width (3), 3.2–3.4; distal width (7), 2.3–2.6; width of shaft (8), 1.0–1.1; depth through internal tuberosity (3), 1.4 mm.

Referred Material.—Coracoid: two lefts, 476 (upper portion), 791 (lower portion). Closest to *C. stellaris*, from which it differs in having (1) head broader, less pointed; (2) coraco-humeral surface shorter, with neck thus less excavated; (3) hook of brachial tuberosity longer. Differs from *C. palustris* in the first two characters; (3) hook of brachial tuberosity deflected toward and closer to shaft; (4) internal sternal facet without shelf.

Ulna: complete right (790) and left (475). Slightly shorter and stouter than in *C. stellaris*. Length, 11.5 mm.

Tibiotarsus: three rights, complete (473), proximal (789), and distal portions (1525). Fibular crest shorter, distal width greater than in *C. stellaris*. Length (1), 21.6; length of fibular crest (2), 2.2; distal width (2), 1.7 mm.

This is the first described fossil species of wren.

Family Icteridae
Genus Pandanaris A. H. Miller

Diagnosis.—Differs from other icterids in having (1) rostrum short and deep; (2) culmen uniformly curved without basal hummock; (3) internasal bridge broad; (4) nasal opening large, one-fourth length of culmen; (5) antero-basal angle of nasal opening 110–125 degrees.

Mandible: (1) lateral aspect of tomium convex throughout; (2) ramus deflected at angle of 160 degrees posterior to horn sheath; (3) external articular process not elongated.

Pandanaris floridana, n. sp.
Text-fig. 1A-D

Holotype.—Rostrum, including premaxillaries (except extreme tip), maxillaries (except maxillopalatine processes), and left nasal (294). From Illinoian stage of Pleistocene at Dixie Lime Products Company mine, one mile southeast of Reddick, Marion County, Florida. Collected by H. James Gut, September, 1952.

Diagnosis.—Similar to *Pandanaris convexa* A. H. Miller (1947, p. 22) of the Pleistocene of Rancho La Brea, but (1) rostrum longer and wider; (2) culmen further overhanging nasal opening; (3) nasal opening smaller; (4) anterobasal angle 110 degrees, instead of 125 degrees. Length of culmen, 23.1 plus; length of nasal fossa, 6.7; greatest depth of nasal fossa, 2.8; width across maxillae at junction with jugal bar, 9.3; anterior width of nasal bridge, 6.5; posterior width of nasal bridge, 5.7; width of nasal bridge under shelf, 5.5 mm.

Referred Material.—Two mandibles (293 and 233–353), both lacking the extreme tip and the right ramus. Compared with *P. convexa*, (1) mandible longer and deeper; (2) dorsal aspect of tomium concave instead of straight; (3) mandibular foramen rhomboidal instead of elliptical; (4) coronoid process produced in a prominent angle. Length from postarticular process, 37.2 plus to 37.3 plus; length from end of postarticular process to posterior margin of horn sheath, 17.7–18.4; maximum length of mandibular foramen, 4.8–5.6; width at gonys (1), 9.1 plus; greatest depth of ramus near base of horn sheath (1), 7.2 mm.

In addition to the bill elements we have collected a number of large icterid limb bones. As more than one species may be represented, they are not referred at the present time.

ASSOCIATED FAUNA

As already stated, the avifauna of Reddick is as yet very incompletely studied. The 52 species of birds which have been identified thus far are listed below, but the indications are that the total list of birds will exceed 60 species. Recent species which are hitherto unrepresented in the fossil record are designated by an asterisk and extinct species by a double asterisk.

Family Colymbidae

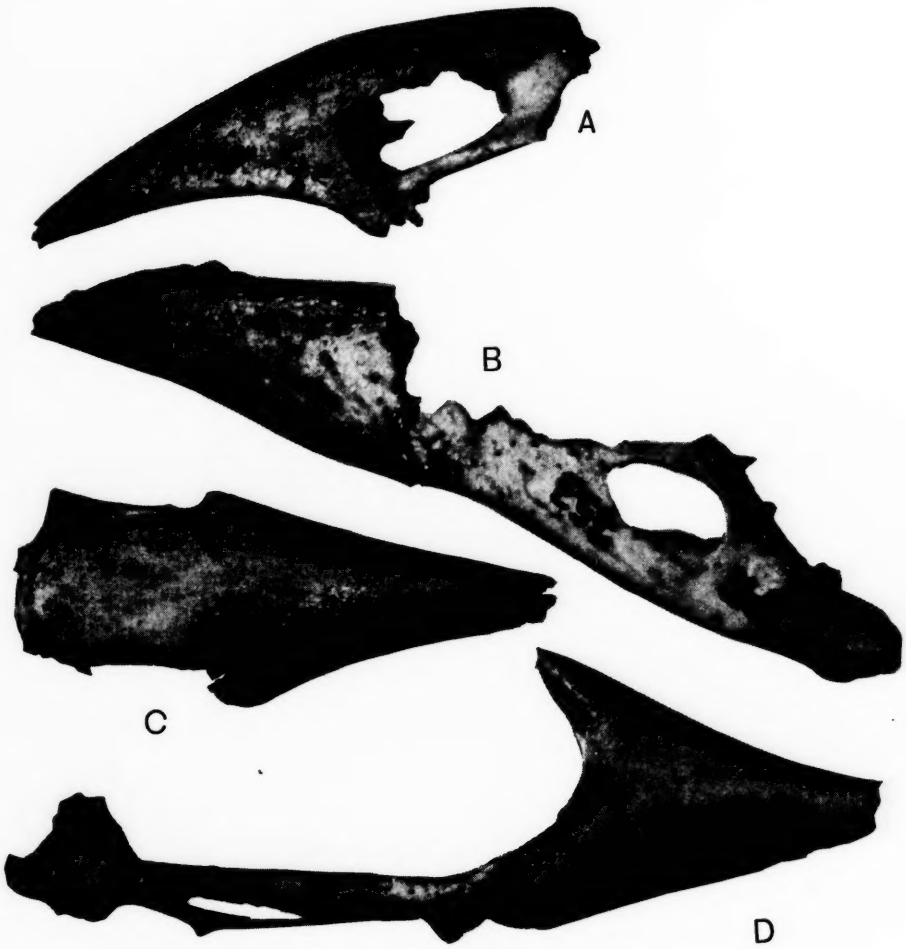
Podilymbus podiceps (Linnaeus)

Family Anatidae

Anas fulvigula Ridgway
Anas acuta Linnaeus
Querquedula discors (Linnaeus)
Nettion carolinense (Gmelin)
Spatula clypeata (Linnaeus)
Aythya collaris (Donovan)

Family Cathartidae

***Gymnogyps amplus* L. Miller
Cathartes aura (Linnaeus)
***Coragyps occidentalis* (L. Miller)



TEXT-FIG. 1—*Panandaris floridana*, n. sp. *A,C*, holotype rostrum, 294; *B,D*, Referred mandible, 233–353. ×3.5.

Family ACCIPITRIDAE

Accipiter cooperii (Bonaparte)
Accipiter striatus Vieillot
Buteo jamaicensis (Gmelin)
Buteo lineatus (Gmelin)

Family FALCONIDAE

Falco peregrinus Tunstall
Falco sparverius Linnaeus
***Polyborus prelutosus* Howard

Family PHASIANIDAE

Colinus virginianus (Linnaeus)

Family MELEAGRIDAE

Meleagris gallopavo Linnaeus

Family RALLIDAE

Rallus limicola Vieillot
Porzana carolina (Linnaeus)
***Porzana auffenbergi* Brodkorb
**Coturnicops noveboracensis* (Gmelin)
***Laterallus guti* Brodkorb
***Fulica minor* Shufeldt

Family CHARADRIIDAE

Charadrius vociferus Linnaeus

Family SCOLOPACIDAE

**Tringa flavipes* (Gmelin)
Capella delicata (Ord)

Family COLUMBIDAE

***Ectopistes migratorius* (Linnaeus)
Zenaidura macroura (Linnaeus)

Family TYTONIDAE

Tyto alba (Scopoli)

Family STRIGIDAE

Otus asio (Linnaeus)
Speotyto cunicularia (Molina)
Strix varia Barton

Family PICIDAE

Colaptes auratus (Linnaeus)
**Melanerpes erythrocephalus* (Linnaeus)

Family TYRANNIDAE

**Tyrannus tyrannus* (Linnaeus)

Family HIRUNDINIDAE

**Progne subis* (Linnaeus)
***Tachycineta speleodytes*, n. sp.

Family CORVIDAE

Corvus brachyrhynchos Brehm
Corvus ossifragus Wilson
***Protocitta dixi*, n. sp.
**Cyanocitta cristata* (Linnaeus)

Family TROGLODYTIDAE

**Troglodytes aëdon* Vieillot
***Cistothorus brevis*, n. sp.

Family PARULIDAE

**Geothlypis trichas* (Linnaeus)

Family ICTERIDAE

***Pandanaris floridana*, n. sp.
Agelaius phoeniceus (Linnaeus)
Quiscalus quiscula (Linnaeus)
Sturnella magna (Linnaeus)

Family FRINGILLIDAE

Pipilo erythrophthalmus (Linnaeus)
**Passerherbulus henslowii* (Audubon)

ECOLOGY

Several species in the above list support the thesis that the two main bone beds are cave deposits. These include the three cathartid vultures, the barn owl (*Tyto alba*), and the swallow (*Tachycineta speleodytes*). Members of all these groups frequently make use of caves and crevices for nesting purposes. The swallow, barn owl, and *Coragyps* are respectively the second, fourth, and fifth most abundant birds in the deposit. They are represented not only by adult bones but also by those from birds too young to fly. There can, therefore, be no doubt that they were interred at their nesting sites.

The exceedingly abundant remains of small rodents and insectivores are attributed to pellets cast by the barn owls. The presence of large numbers of bats (*Myotis* sp.) is also an indication of the cavernous nature of the deposit. Such a habitat would also form a suitable situation for the mammalian carnivores, of which a number in addition to those listed above occur in the deposit.

The avifauna is fairly typical of a wet grassland or fresh water marsh community. The pied-billed grebe (*Podilymbus podiceps*), the six species of ducks, the six species of rails, the killdeer (*Charadrius vociferus*), snipe (*Capella delicata*), lesser yellowlegs (*Tringa flavipes*), burrowing owl (*Speotyto cunicularia*), sedge wren (*Cistothorus brevis*), yellow-throat (*Geothlypis trichas*), red-winged blackbird (*Agelaius phoeniceus*) meadowlark (*Sturnella magna*), and Henslow's sparrow (*Passerherbulus henslowii*) in particular are characteristic of such a community. The remaining species, although of somewhat wider tolerance, are also in harmony with a marsh community.

The marsh appears to have contained no sizeable body of open water and probably was not fed by a permanent stream. There is an absence of birds which are confined to deep water, and the total absence of fish remains eliminates a permanent body of water. It would therefore appear that the marsh became dry periodically, and a fluctuation of the water table would also account for the stratification of the bone bed.

ZOOGEOGRAPHY

The only species of birds from Reddick which are absent from the present avifauna of Florida are the 11 extinct species listed above. Five of these have their closest affinities to the southwest, five to the north, and one is of uncertain relationship.

Porzana auffenbergi was described from Haile, Florida, from a Pleistocene deposit which I now believe to be of Illinoian age and thus contemporaneous with the Reddick deposit. Since it has left no descendants in the present fauna, its relationships and ecological requirements are uncertain.

The group which has its affinities to the Pleistocene or Recent fauna of the southwest includes *Gymnogyps amplus*, *Coragyps occidentalis*, *Polyborus prelutosus*, *Protocitta dixi*, and *Pandanaris floridana*. The

first three have their type localities in the Pleistocene of California.

The California condor (*Gymnogyps californianus*), is the living descendant of *G. amplus*. The California condor is presently confined to California, although within the last 3000 years it occurred eastward as far as Texas (Wetmore & Friedmann, 1933, p. 37). This is undoubtedly a reflection of the retreat of the genus from its Pleistocene continent-wide distribution.

The living representative of *Coragyps occidentalis* is the black vulture (*C. atratus*). This species occurs on the American mainland from Argentina north to Mexico, and into the southeastern United States. Although only casual today west of Texas, 2000 years ago it occurred in New Mexico (Wetmore, 1932, p. 141), and *C. occidentalis* is known from several Pleistocene localities in California. It would thus appear that this genus also has had its range restricted since the Pleistocene.

Audubon's caracara (*Polyborus cheriway*) is the living representative of *P. prelutosus*. It occurs in tropical American north to Arizona and Texas, with an isolated colony in southern Florida. It does not reach the latitude of Reddick, although 125 years ago it occurred as far north as St. Augustine (Burns, 1909, p. 103). The Pleistocene *P. prelutosus* had a range extending from California to Florida. Thus the genus *Polyborus* has likewise been restricted geographically during comparatively recent times.

The genera *Protocitta* and *Pandanaris* are extinct. The closest relatives of *Protocitta* are the living Mexican and Central American jays of the genera *Calocitta* and *Psilorhinus*. *Pandanaris* is known from two Pleistocene species, one in California and one in Florida. Its closest surviving allies are the cowbird genera *Tanganavius* and *Molothrus*. The latter genus occurs almost throughout North and South America, but *Tanganavius* is a Central American genus, extending northward only to Texas and Arizona.

Thus all five genera belonging to the group of southwestern affinities may be regarded as representatives of an arid subtropical or Sonoran fauna, which has recently withdrawn from parts of the northern boundary of its range. Two genera of this group survive in the present day fauna of Florida, and one of them presently has a discontinuous distribution.

The mammalian fauna of Reddick likewise shows a strong southwestern influence in the several genera of edentates. In the case of both the birds and mammals, it would appear reasonable to assume that the southwestern element in the fauna reached the east during the warm and dry climatic conditions of the Yarmouth or Aftonian interglacial stages, or even during late Tertiary. Climatic deterioration during the glacial stages and the repeated insularity or inundation of much of Florida during the interglacial stages both undoubtedly contributed to the partial extermination or restriction of this fauna.

The group of Reddick birds with affinities toward the north includes *Laterallus guti*, *Fulica minor*, *Ectopistes migratorius*, *Tachycineta speleodytes*, and *Cistothorus brevis*. The descendants of all these boreal species occur as winter visitants in northern Florida, or did so within historical times. It is perhaps more than an accident that whereas the southwestern group is composed of non-migratory forms, the northern group consists entirely of birds whose descendants are migratory.

The recently exterminated passenger pigeon (*Ectopistes migratorius*) formerly wintered south at least to Alachua County, adjoining Marion County to the north; it bred from Canada south to northern Virginia. *Laterallus guti* has its closest living ally in the black rail (*L. jamaicensis*). The black rail breeds from Canada south to Illinois and North Carolina, with isolated populations in Florida, California, Jamaica, Peru, and Chile. *Fulica minor* was described from the Pleistocene of Oregon. It is the temporal representative of the living American coot (*F. americana*), which in the east breeds from Canada south regularly only to New Jersey. The present representative of *Cistothorus brevis* is the sedge wren (*C. stellaris*), which breeds from Canada south to Delaware.

In the absence of knowledge of the breeding of these four species at Reddick, it

should perhaps be emphasized that this portion of the northern element does not afford strong evidence for a much cooler climate during the Illinoian stage. Among fossil birds of migratory groups such evidence can be obtained only if young bones are available. Many young bones of the swallow (*Tachycineta speleodytes*) have been collected. The closest living relative of *T. speleodytes* is the tree swallow (*T. bicolor*), a boreal species which reaches the southern limit of its breeding range in Virginia.

A similar northern element among the mammals of Reddick appears in the lemming (*Synaptomys australis*), a member of an essentially boreal group. In the lowlands today the genus *Synaptomys* finds it southern limits in Maryland, with an isolated population in the Dismal Swamp of Virginia and North Carolina (Miller and Kellogg, 1955, p. 562).

The question has often been raised as to how far the effect of cooling would have been felt in front of the Pleistocene glaciers. Because of the distributional pattern of the northern genera in the Reddick deposit, I feel safe in suggesting that the climate in northern Florida during the Illinoian glacial stage was at least as cool as that of Virginia today.

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REFERENCES

AUFFENBERG, WALTER, 1955, Glass lizards (*Ophisaurus*) in the Pleistocene and Pliocene of Florida: Herpetologica, vol. 11, p. 133–136.

BRODKORB, PIERCE, 1952, A new rail from the Pleistocene of Florida: Wilson Bull, vol. 64, p. 80–82, 1 fig.

——, 1954, Another new rail from the Pleistocene of Florida: Condor, vol. 56, p. 103–104, 1 fig.

BURNS, F. L., 1909, Audubon correspondence: Wilson Bull., vol. 21, p. 103–104.

CABANIS, JEAN, 1850–1851, Museum Heineanum: part 1, p. i-vii, 1–234. (R. Frantz, Halberstadt.)

COOKE, C. W., 1945, Geology of Florida: Florida Geol. Surv., Geol. Bull. 29, p. i-ix, 1–339, 1 pl., 47 text-fig.

COUES, ELLIOTT, 1878, Birds of the Colorado valley: U. S. Geol. Surv. Terr., Misc. Publ. 11, p. i-xvi, 1–807, 65 fig.

GOIN, C. J., & AUFFENBERG, WALTER, 1955, The fossil salamanders of the Family Sirenidae: Bull. Mus. Comp. Zool., vol. 113, p. 497–514, 2 fig.

GUT, H. J., 1939, Additions to the recorded Pleistocene mammals from Ocala, Florida: Proc. Florida Acad. Sci., vol. 3, p. 54–55.

LAMBRECHT, KALMAN, 1933, Handbuch der Palaeornithologie: p. i-xx, 1–1024. (Gebrüder Borntraeger, Berlin.)

MACNEIL, F. S., 1950, Pleistocene shore lines in Florida and Georgia: U. S. Geol. Surv. Prof. Paper 221-F, p. 95–107, pl. 19–25.

MATSON, G. C., & SANFORD, SAMUEL, 1913, Geology and ground waters of Florida: U. S. Geol. Surv. Water-Supply Paper 319, p. 1–445, map.

MILLER, A. H., 1947, A new genus of icterid from Rancho La Brea: Condor, vol. 49, p. 22–24, fig. 4.

MILLER, G. S., JR. & KELLOGG, REMINGTON, 1955, List of North American Recent mammals: U. S. Nat. Mus. Bull. 205, p. i-xii, 1–954.

WETMORE, ALEXANDER, 1932, Additional records of birds from cavern deposits in New Mexico: Condor, vol. 34, p. 141–142.

——, & FRIEDMANN, HERBERT, 1933, The California condor in Texas: Condor, vol. 35, p. 37–38.

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ORIGIN OF CHELICERATES

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ABSTRACT—All classes of chelicerates are claimed as closely related, and as the only other arthropods that have arisen from the trilobites (Raw, 1925, 1953). They are derived from the pre-Cambrian ancestors of the metaparial trilobite family, Olenellidae. As only the external features of Trilobites can be studied directly, consideration is largely limited to such. The prosoma of the chelicerates without the pre-genital segment is claimed as the exact equivalent of the heads of the Trilobite and of all the other arthropod classes: this is the only tagma that all have in common. Chelicerate evolution commenced when members of that trilobite family discovered the river estuaries, up which they travelled, burrowing through the surface mud and swimming through the water. In this way they learned to ascend the rivers, and to reach the upland lakes. Much deployment of the classes is deduced to have occurred in pre-Cambrian time. Their evolution was extensively controlled by a triadic periodicity in their segmentation (triadic merocyclism). This is deduced also to have characterised the protarthropod and the deutarthropod, from which the trilobite had been evolved. Owing to this, different "classes" esulted: with 15, 12, 9, 6, and ?, 3 or 0 significant post-cephalic ("abdominal") regments (Raw, 1953), the last significant segment in each "class" being a macrosomite, the 15th, 12th, 9th, or 6th, etc., post-cephalic segment. In each the anus sended to shift to the last significant segment, and the segments behind this tended to be greatly reduced, being represented today by a flagellum or other teduction, or to disappear by failure of development. The anus is thus secondary rn chelicerates, the hind-gut is practically non-existent, and there is no telson.

i In the lakes a new period of evolution would begin which was followed later by invasions of the land, but by a return to the sea by the Xiphosura. Very early the mode of life of the river bed had fixed the position of the reproductive organs and caused the entire loss of all ambulatory function from the post-cephalic appendages. The chelicerate was thus most severely handicapped for locomotion on land. To this handicap can be attributed three important effects: (1) the loss of the compound eyes, and the use of the three classes of simple eyes instead, (2) the carriage of the body by the "head" limbs, (3) the strange cannibalism that affects the spiders, scorpions and opiliones, and possibly, (4) the lack of wings.

One new order, Beckwithida, is proposed.

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1. INTRODUCTION

Text-fig. 1–3

THE origin of the animal phyla and the relations of the classes within them are now little studied, except in the vertebrates, where, besides their comparative anatomy and development, we have the evidence of their successive appearance in the paleontological record.

The origins and deployment of the invertebrates occurred mainly further back in geological time, and therefore earlier even than the fossil record. It is, however, the writer's view that, in the anatomy and ontogeny of modern forms, combined with what the geological record supplies of fossil forms, there exists the evidence for very definite and firmly based conclusions—much more extensive than have hitherto been advanced. Such an outlook, too, is of great importance for the proper advance of zoology.

Thanks to Professor Lapworth it fell to

the writer's lot near the beginning of the century to study intensively the Cambrian trilobites and among them the members of the trilobite family Olenellidae, which on both sides of the north Atlantic, characterise the oldest marine fossiliferous rocks. So important are they in defining their range as to have given their name to this Lower Cambrian rock series—the Olenellidian—which are successively overlaid by the Paradoxidian and Olenidian, the three together comprising the Cambrian System.

What struck the writer most forcibly in that study were the very close comparisons that could be instituted between members of this single family of trilobites, the Olenellidae, and the widely ranging members of the chelicerates. The writer was so impressed, that already in 1924 he lectured before the Birmingham Natural History and Philosophical Society on "The Origin of the Arachnid." In the same year he distinguished three types of head plan in primitive trilobites, which he called proparial (after Beecher's division Proparia), mesoparial and metaparial, only the Olenellidae being proved metaparial (Raw, 1924; 1925, p. 307–308, etc.), and all three were derived from a common original type, the heptacicephalic, of greater antiquity. At the same time the conclusion was cryptically announced that the Olenellidae had given rise to the arachnida in the words: "it is only the metaparial among known Trilobite families that can be claimed to have any recent descendants" (1925, p. 312).

Since the metaparial was more opisthoparial than were the members of Beecher's "Opisthoparia" it entailed a change of name from opisthoparial to mesoparial. The views expressed below can consequently be claimed as mature conclusions on one of the interests of a lifetime. What especially interested the writer in his study of Cambrian trilobites was their ontogenies and he claimed that these well illustrated the truth of the Biogenetic law. At the same time his conclusions were entirely different from those of G. F. Matthew, C. E. Beecher, and P. E. Raymond, who previously had claimed that they did so and indeed had based their classification upon their interpretation of the ontogenies. The writer claimed that all trilobites had been derived from a heptacicephalic ancestor and that modifications of the glabella had preceded the divergence into proparial, mesoparial and metaparial forms (1925, p. 285–286, 310–316; 1927, p. 131–143).

The present paper is devoted to a demonstration of the very close parallels that can be instituted between the Olenellidae and the chelicerates and to a discussion of their significance. It is claimed that these trilobites demonstrate conclusively the mode of origin of the chelicerate in pre-Cambrian time, from the ancestors of this trilobite family, and how they deployed into the variety of orders; some with a considerable number of abdominal segments like the scorpion and the eurypterid, the bulk of the arachnids, believed to have 12, others with less like the xiphosures, and still others very few, like the mites and ticks (Acarina) and even the pycnogonids.

Part of the long evolution which preceded that of the chelicerate has already been discussed by the writer in two recent papers. In "The External Morphology of the Trilobite and its Significance" (Raw, 1953), the writer traced the evolution of the trilobite class from the polychaet through three intermediate stages; namely, (1) the proarthropod, which preceded the evolution of the arthropod head, (2) the protarthropod, furnished only with simple eyes before the evolution of the compound eye; and (3) the deut-arthropod with compound eyes. In the same paper it is claimed, contrary to current opinion, that all true arthropods have fundamentally the same cephalic or prosomatic tagma; in other words, that the cephalon of the trilobite, which itself was antennate, is not only the same in somatic constitution as the heads of the "antennate" or "mandibulate" arthropods, but is also exactly the same as the prosoma of the chelicerates, without however the pre-genital segment, which is now recognised by all as belonging to the abdomen. In other words both mandibulates and chelicerates have the same head or prosomatic tagma; and whereas the mandibulates all walk on their post-cephalic limbs, the chelicerates walk entirely on their cephalic. It is stated also that, of modern

arthropods only the chelicerates are descended from a trilobite, and that this was in pre-Cambrian time. Because of this, part of the chelicerate evolution was also dealt with incidentally in that paper, for naturally comparisons between them elucidated both.

In the earlier paper referred to (Raw, 1949) the evolution of the primitive polychaet was discussed. The respective evolutions of the brain, of the visceral nervous system and of the stomodeum were claimed to be closely related, and highly complex; the brain and visceral nervous system having grown at the expense of the central nervous system at each increase in the stomodeum.

For the subject matter discussed in this paper the writer is indebted not only to the numerous writers mentioned in the list of literature, but more especially to Prof. A. Petrunkevitch for the gift of his recent papers, to Prof. L. Størmer for his very numerous paleontological papers, and to Prof. L. J. Wills for his papers on fossil scorpions and for access to his library. All these are deeply thanked for the stimulus furnished by their work. This paper unfortunately opposes in some ways the first two authors just mentioned, but had the writer agreed with them in all points, it would never have been written.

2. TRILOBITE, CHELICERATE AND ARACHNID
Text-fig. 1–3,6,7,9

Regarding the Arachnida, great diversity of view has been expressed within the last half century as to what should be included under the term. In contrast, trilobite and chelicerate are much more definite and stable entities.

Many have used the term arachnid as the equivalent of chelicerate; others have greatly restricted it, whereas Lankester extended it. As late as 1949 two sets of works dealing especially with the Arachnida have been published, in France and in the U.S.A., respectively. In France, Tome VI of Traité de Zoologie directed by Prof. P. P. Grassé (1949) embraces the chelicerate classes, the various orders of which are discussed by French specialists, whose work is much used below. In this the "Généralités" on the Arthropoda by Prof. A. Vandel contains the classification of the arthropod phylum there adopted. Omitting the appended groups of onychophores, tardigrades and linguatulids, it is:

	Sub-phyla	*Classes*
I Proarthropods	Trilobitomorphs	Trilobita and others
II Euarthropods	Chelicerata	Merostomata
		Arachnida
		Pantopoda
	Mandibulata or Antennata	Crustacea
		Myriapoda
		Insecta

It is followed by a more detailed subdivision of the chelicerates (Vandel, 1949, p. 153, 154).

In the present connection it is of interest to note that the trilobites are even excluded from the euarthropods and that the Arachnida exclude the merostomes and the pantopods as is now usual.

The use there of the word proarthropod is surely unwise: the word should signify the evolutionary stage preceding that of the arthropod, as the writer has used it (Raw, 1953). (See Text-fig. 6.)

The anterior tagma of the arthropods.—The order of the subphyla given by Vandel is undoubtedly the correct one, and is in contrast with previous classifications; but he does not realise why. It is because, as the writer claims, all arthropods have the same anterior tagma, the only tagma which they have in common; and their classification should depend on the primitive or specialised character of this tagma, which is most primitive in the trilobita and most specialised in the mandibulata. This last is a much better term than antennata, because both trilobita and mandibulata have antennae, but only the last named are known to have mandibles.

The chelicerates are defined (Vandel, 1949, p. 217) as: Arthropods furnished with a single pair of jointed preoral, but originally postoral, appendages, generally with prehensile function. The 2nd pair of appendages is postoral, originally of ambulatory type: as the pedipalps, these are transformed into appendages of prehensile, sensory or masticatory function due in this case to gnathobases. The anterior region of the body or prosoma has no equivalent in the other

arthropods, and results from the fusion of the preoral segments with 6 or 7 postoral. The genital ducts open on the 8th segment.

This definition is incomplete in not mentioning the last four prosomatic appendages. But more important, it is quite wrong, the writer claims, in stating that the prosoma has no equivalent in the other arthropods.

This belief in a more extensive metamerism of the anterior tagma of the chelicerate is the view perhaps universally held up to the present. But the writer (1953, p. 87–90, 125–127) has claimed that primitive trilobites indicate clearly what somites were involved in the origination of the head of the arthropod; for the habitual subretroversion of the prostomium and peristome of the ancestral pro-arthropod, in its new mode of feeding, led to the formation of the head all at one time, out of those subretroverted and therefore ventral parts, together with the succeeding six normal segments, whose terga were still dorsal.

This complex head was inherited by all the arthropods, whose heads are indeed the strict equivalent of the prosoma of the chelicerate. The prostomium became the labrum (hypostome of trilobite) and its appendages were lost; but the eyes are represented by the nauplius eyes of crustacea and their homologues in other arthropods. The appendages of the peristome are the antennae (or 1st antennae in crustacea); further, a pair of eyes belonging to this "segment" is represented in modern arthropods. The appendages of the six normal segments that succeed were handed down, as also six pairs of eyes on these segments. All their six pairs of appendages were retained (in such a form as can easily be recognised as appendages) only by the chelicerates, as explained below; but these lost the antennae from the preceding "segment." In other modern arthropods some of the appendages morphologically behind the peristomial antennae were reduced under cover of the labrum, within what became a new, anterior extension of the gut (Raw, 1953, p. 107–113).

On this view the chelicerate is, in its head or prosoma, the most primitive of all modern arthropods, and has to walk on its cephalic limbs, simply because in its ancestors all possibility of *ambulatory* function had been entirely lost by the appendages of the postcephalic segments. If the writer's view is accepted, and if it be true, as seems probable, that there are no direct descendants from the prot-arthropod stage, the natural order of the subphyla would be I Trilobita, II Chelicerata, III Mandibulata (Raw, 1953, p. 122–124).

The old view is illustrated by the "Diagnosis" of the trilobitomorphs, which includes the trilobites in the same work (Størmer in Grassé, 1949, p. 159). It is:

> Primitive aquatic arthropods with a cephalon almost always furnished with 4 postoral somites, possessors of preoral antennae, the other appendages being biramous, of Trilobite type.

Contrast this with the chelicerate, and yet the claim is confidently made by the writer that both have the same constitution of head: that, indeed, a trilobite head became the Chelicerate prosoma.

It is evident that paleontologists have not done their duty. Størmer homologises the four *posterior* segments of the cephalon of the protaspid larva of *Elliptocephala*, an olenellid trilobite, with the four *anterior* appendage-bearing segments of the embryo of *Limulus* (Iwanov's "larval somites") (Størmer, 1944, fig. 2, p. 19). He is followed by Vandel who numbers I–IV the *posterior* four segments of the protaspis cephalon of *Liostracus linarssoni* and homologises them with the same so-called larval somites of *Limulus*. In both these trilobite larvae the two segments of the dorsal shield in front of the four mentioned are not defined at that stage. Their lack of development can be attributed to the reduction and modification of their appendages, covered in, as they were, by the ventral hypostome or labrum. Størmer claims that the two segments are a single one, the antennal segment, homologous with the first-antennal or antennular of crustacea; that the appendages of the head of the latter belong to consecutive segments of the ancestor; and that the prosoma of the chelicerate has two or three extra somites behind. The writer, on the contrary, homologises these two anterior glabellar segments with the cheliceral and pedipalpal segments of the arachnid and the four posterior segments with those bearing the walking legs of the arachnid or in each case the

corresponding segments of *Limulus* (Størmer 1941, 1944; Raw 1953, p. 123–127).

The second series of recent papers, above referred to, is by A. Petrunkevitch comprising "A Study of Paleozoic Arachnida," his article Arachnida in the 1947–49 Encyclopaedia Britannica, and about the same time his articles on spiders, scorpions, Xiphosura and Eurypterida in the same.

Petrunkevitch, like the French authors in the Traité, also excludes the Merostomata and Pycnogonida from the Arachnida (1948, 1949); though in 1913 he had to some extent included the Merostomata in it (Petrunkevitch, 1913, p. 28).

Gerhardt (1935), also, in the Kükenthal-Krumbach Handbuch defines the Chelicerata, which there excludes the Pycnogonida (= Pantopoda); and he divides them into two classes—I "Marine," Merostomata; and II Terrestrial, Arachnida.

This then is the modern view: all the terrestrial chelicerates are gathered in the Arachnida, which excludes all aquatic forms. To the writer this seems most arbitrary: it is like referring the trunk or the root of a tree to a different genus from that of the branches, leaves and flowers of the same. This classification is opposed below, because of the belief that, only by including modern and extinct aquatic forms can we at all connect the orders of the recognised Arachnida. There is, the writer believes, much closer relationship between the Eurypterida and the scorpions, and between the Xiphosura and certain Carboniferous reputed arachnids, than there is between the scorpion and the other modern arachnids. For this reason the scope of this paper is extended beyond the recognised Arachnida.

At the opposite pole from the modern view was that of Lankester (1910). Within his subclass Arachnida he included not only the terrestrial forms, but also the aquatic Xiphosura and Eurypterida; and within his class Arachnida, not only these, but also the subclass Pantopoda, together forming his Grade B, Nomomeristica; whereas his Grade A, Anomomeristica was the Trilobita, believing as he did that their uniramous antennae were homologous with the chelicerae of the arachnids. This was the view generally held then, and is that of Börner (in A. Lang's textbook, 1921 and in Borradaile et al. 1935, 1941).

Petrunkevitch (1913) suggested the homology of the second antennae of Crustacea with chelicerae; and Hanström (1928), on the basis of comparative studies of the nervous systems of modern arthropods, did the same. If this homology, which the writer accepts, is correct, we have in the trilobites no evidence whatever as to the nature of the homologue of the chelicerae of chelicerates. Lankester's inclusion of the Trilobita in his Arachnida must have been due to a strong belief that they were closer akin to the Arachnida than to any other modern class; but he did not see how.

The writer, accepting Hanström's homology of the 2nd antennae with chelicerae, believes that in the Malacostraca the next two pairs of appendages were reduced under cover of the labrum within an anterior extension of the alimentary canal, and may be represented by the gastric mill (1953, p. 126).

Though the purpose of this paper is to demonstrate that trilobites in pre-Cambrian time gave origin to the chelicerates, there is no reason to suppose that any known form had chelicerae; and they are best assigned to a separate class.

The grouping of all terrestrial chelicerates into a class called the Arachnida has resulted in a valiant attempt to see unity in the diversity—as great a unity as is apparent within the Insecta and the Malacostraca. Petrunkevitch (1948a) summarises the scope, characteristics and classification of the class. Dividing the old order Pedipalpi into the three divisions distinguished by Pocock and Kästner, he makes the class comprise 16 orders of which five are extinct and limited to the Paleozoic rocks. Regarding the segmentation he states

> it is generally accepted that their embryo is composed of the same number of somites . . . no matter to which order the embryo belongs . . . The number of segments as seen in an adult arthropod is never the same as in its embryo. Arachnida are no exception to this rule . . . Presumably that number (of somites) is 21 for all Arachnida . . . The abdomen is just as certainly composed of 12 somites. This original number is retained in the adult segmentation of Thelyphonida, Phrynychida and Pseudoscorpiones, as well as in the Liphistiomorph spiders.

Where less than 12 are detectable in the abdomen, he attributes it to subsequent reduction; and because the scorpion, when we count the pre-genital, exhibits 13, both Buxton and Petrunkevitch claim that there has been subdivision of the 8th abdominal somite. Below, on the contrary, it is argued that just the opposite kind of change has occurred, though not in the same place.

In contrast with the scorpion are the acari, the more primitive of which (e.g., the the tick genus *Amblyomma*) clearly displays evidence of six sub-equal abdominal segments, with room for no more. This is only half the standard number; but doubtless it will be supposed that this is due to reduction from the standard 12. This same view of the derivation of all the variations of abdomen, from a 12-segmented original, Petrunkevitch repeats (1949).

Professor J. Millot, more cautious, in his "Definition" of the Arachnida (in Grassé, 1949, p. 264) says nothing as to the number of the abdominal segments, and later (p. 268) acknowledges that it varies sensibly from one order to another. Comparisons with the trilobite family Olenellidae suggest, however, that, far from 12 being the standard number for these 16 orders of Arachnida and the other orders within the Chelicerata, the number was very varied. Below, it is claimed that the primitive number of fully functional abdominal segments was in different orders 15, or 12, or 9, or 6 or less within the chelicerates. And that even in the modern terrestrial "Arachnida" the number includes 15, 12 and 6. This is another of the characters in which the subphylum is unique.

Besides this enormous variation in the apparent and the ancestral number of somites, we have also the existence or not of either a tail spine or a flagellum, and the similarly great variation in the respiratory organs. And besides these, again, are the numerous features in the internal anatomy in which the chelicerates are unique, and of which only a few can be considered here.

The tail spine of the xiphosure, the terminal spine or plate of the eurypterid, and the sting of the scorpion are by all writers placed in the same category. Petrunkevitch calls it a "telson"—"a dorsal post-anal outgrowth of the body wall articulated to the anal segment." Fage also calls it a telson; but states (Grassé, 1949, p. 221) that development shows that it is not a true telson, that it does not correspond to the segment behind the generative zone, but represents in reality the *coalesced tergites* of *several rudimentary segments*. Elsewhere he makes it the 8th abdominal segment; but agrees that it may be the 15th as in *Olenellus* (p. 245)! In the same volume Vandel (p. 94-95) defines the telson by saying that the pygidium of the annelids is represented in the arthropods by the telson. This carries the anus, and is devoid in actual forms of nerve ganglia and of coelomic cavities. Comparison with the trilobite given below proves conclusively, however, that in its origin the tail spine had nothing whatever to do with the terminal anal "segment" or analite of the ancestral annelid, and that it represents only a single segment originally very far in front of this.

Turning now to the very different flagellum: the views of arachnologists are definite and in agreement. Flagella, where they occur (in Palpigradi, Thelyphonida and Schizomida), are by all writers homologised with one another. Petrunkevitch, as mentioned, calls the flagellum also a telson. Millot (1949, p. 536) expresses the same view. Of the Palpigradi he states that

> the 11th abdominal segment bears the anus and is prolonged as a remarkable flagellum, almost as long as the rest of the body. It has about 15 joints, and has the value of a telson. It is mobile and in the living animal is often erected perpendicularly.

Again of that in the Thelyphonida he writes:

> the anal segment gives origin to a long slender flagellum. . . . It is a case of a simple prolongation of a segment which can be homologised with the caudal flagellum of the Gigantostraca [he must mean the tail spine] or to the sting of the scorpion; and the joints, which constitute it, devoid of muscles, have not at all the value of atrophied segments of the body.

But the "segments" of the flagella are closely comparable in length with the posterior abdominal segments of the arachnids that carry them, and it will be demonstrated how comparison with the trilobites proves conclusively that, contrary to the above

cited views which make the whole flagellum merely a part of the telson or analite, its separate parts are indeed post-abdominal segments of the body, though much reduced; and further, that they have no homology whatever with the tail-spine of the merostomes, the sting of the scorpion, or the telson.

Reason will be given for the view that the terrestrial "Arachnids" are a composite group, in which some have 15, others 12, and still others 6 somites behind the prosoma, while also some but by no means all of those with 12 have besides a considerable number of reduced segments. We are therefore fully justified in including also in our survey the merostomes, for these embrace forms with 15, 12 and 9 somites behind the prosoma and some of these also have greatly reduced segments besides those which are normal. But in no chelicerate can other than greatly modified posterior segments be found, and therefore for our survey to be complete the olenellid trilobites must also be considered, as here the posterior segments are more normal.

The extremely varied numbers of segments which arachnids exhibit may be attributed not only to the early range due to merocyclism but also to their many modes of life involving various reductions.

Also though there is good reason to believe that no known trilobite was ancestral to modern "Arachnida," seeing we have none older than the Cambrian; and whether or not any known merostome was closely connected with any arachnid, there can hardly be two opinions now as to the derivation of terrestrial forms from aquatic freshwater forms and those ultimately from marine. This is another reason why we should include the aquatic forms.

Among these the Pantopoda should be included. According to Størmer, who follows Iwanov, the Arthropoda are polyphyletic arising by four stems from the annelids! These stems are in order, the Myriapoda-Insecta, the Trilobita-Chelicerata, the Crustacea, and the Pantopoda (Størmer, 1944, p. 143, 148). These last he thus separates from the chelicerates, and states (p. 147) that "the morphology of fossil and recent Pantopoda shows little resemblance to that of the Arachnomorpha."

On the contrary the pantopods show close affinity with the chelicerates and are included in them by others. How otherwise could one explain the normal association of chelophores with four pairs of walking legs and with no further appendages behind these? The so-called palpi the writer would closely associate in origin with the chelophores as they are closely associated in position on the animal. It is usual to regard the palpi as homologous with "pedipalpi" and the ovigerous legs also as representing a segment which would make the ordinary pantopods with 4 pairs of walking legs have seven pairs of appendages. But one must remember that all the 6 normal appendages of the arthropod cephalon would originally be biramous, and further that these animals are now highly specialised, as is indicated by their entire loss of pleura, their extreme subdivision of the cephalon or prosoma and indeed their every feature. Merocyclism offers an explanation of their body being limited to the prosoma.

How to account for the fifth pair of walking legs of the Decolopodidae, and the still more numerous appendages more rarely found is a problem, but a repetition-sport would be a possible origin.

It does not seem too difficult to imagine the evolution of the pycnogonid from an early chelicerate by an early return to the sea, indeed in pre-Cambrian time. So subdivided a body does not need respiratory organs; and pantopods are not unique in having viscera extending into the appendages. Like other groups, chelicerates have suffered strange degenerations in response to particular modes of life, but these will not be considered.

Turning now to the restricted "Arachnida," these as at present constituted are not a connected group, and do not constitute a subphylum. They are an association of those terminal chelicerate branches that attained terrestrial life. Only by including known and unknown aquatic forms could we at all make of them a rooted natural phylum.

A comprehensive paper on this subject would be very long, but zoologists will now agree that the different orders of chelicerates have all had aquatic ancestors, if we go back far enough. Hence, in most cases it will be sufficient if the origins of the various types

of the known aquatic forms are deduced, and many terrestrial forms merely receive mention.

3. CONTRIBUTION OF THE TRILOBITE
Text-fig. 1–6,7a

The writer's views are based mainly on the characters of Cambrian trilobites. Had the paleontological record begun later, these conclusions could perhaps never have been reached, because they are suggested by the most primitive trilobites of that earliest geological system. The known Olenellidae and Paradoxidae limit themselves absolutely to the rocks of the Lower and the Middle Cambrian respectively; and the Olenidae are almost limited to the Upper Cambrian. It is these and other most primitive families that indicate the origin of the class from the polychaet, and shed a flood of light also on the origins of the other arthropod classes.

All the segmental organs of the trilobite would be inherited from the pro-arthropod and behind this from the polychaet. So also was merocyclism (a periodicity in the segmentation) exhibited now in polychaets only by the Polynoidae. In this family it consists in the regular incidence of segments bearing elytra instead of dorsal cirri, segments called by the writer macrosomites. In the subfamilies Polynoinae and Hermioninae their incidence divides the body into groups of two segments from the front back to normal segment 22, and groups of three behind this—diadic and triadic merocycles.

The body of the polynoid in those subfamilies consists in order of prostomium and peristomium followed by the normal segments, of which the macrosomites are numbers 1, 3, 4, 6, 8 and all even numbers to segment 22 and then every third segment.

The particular distribution of diads and triads indicated as characteristic of the ancestor of the olenellid trilobite could be imagined to have arisen from that of these polynoids after the evolution of the arthropod head. For this may well have been followed by the advance of the triads from segment 22 up to the head. This indeed is much easier to imagine than is the origin of the actual distribution in those polynoids. The distribution suggested by the Olenellidae is of importance because it explains not only the mode of evolution of this family, but also that of the Chelicerata, the Crustacea and the Insecta. But the macrosomites in the ancestor of these arthropods were specialised by a tendency to larger size and larger pleural and axial spines.

Between the Polychaeta and the Trilobita the successive stages of the pro-arthropod, the prot-arthropod and the deut-arthropod have been deduced (Text-fig. 6).

The pro-arthropod was like a polynoid in segmentation, but its limbs were already arthropodan and triramous in character consisting of pleuron, endopodite and exopodite (Raw, 1953, p. 83–87, 119–121). Also its pleura and the dorsal surface of the axial lobe were furnished with strengthened cuticle, and all segments bore eye-spots and axial spines. The adult was apparently a walker on the sea floor.

The arthropod originated by the adoption of a new mode of feeding. The prostomium and peristome were subretroverted, and their terga became the "hypostome" or labrum, and the "rostrum," respectively; and the following six normal segments became associated with them in serving the mouth. These eight parts came to form the head, which was furnished with 9 pairs of simple, eyes: 2 pairs on the prostomium (Class I), 1 pair on the rostrum (Class II), and 6 pairs on the 6 dorsal segments (Class III). There would be also 4 pairs of greater pleural spines on macrosomites 1, 3, 4 and 6. Later the terga of these segments coalesced to form the head and the adjoining spines on the pleura of normal segments 3 and 4 coalesced into what became the parial spine of the trilobite. This was at first heptacicephalic, with 3 pairs of lateral (pleural) spines and an occipital on the head, the segmental axial spines in front of this aborting. These two are the prot-arthropod stages.

Later, after the compound eye was evolved, the deut-arthropod stage was reached. This had 10 pairs of eyes on its head, the compound eye constituting Class IV. These eyes would supersede the 6 pairs of Class III eyes in the ontogeny, as is suggested by *Limulus* and the insects. Besides these there would be post-cephalic simple eyes (Text-fig. 6).

The most important of the inherited segmental features for the present purpose are the segmentation and its merocyclism, the

eyes, the dorsal axial spines, the biramous appendages and the pleura, which also were *appendages moved by muscles*, and which bore the segmental eyes. The pleura ended in pleural spines, the size of which as also of the dorsal axial spines was determined by the merocyclism. The earlier arthropods were marine like the trilobites, and the presence of long spines on the macrosomites would be of great value for flotation during the pelagic larval life (Text-fig. 1A,1C); but any spines directed forward might be a great hindrance to progression on the sea floor and other surfaces.

The divergence of the trilobite from the deut-arthropod has been attributed by the writer to their habit of seeking protection of the delicate ventrum inherited as such from the pro-arthropod, by closely apposing this to a surface, e.g., the sea floor. With this was associated slower locomotion than that of other groups. Adaptation to this habit of close apposition led to the evolution of the semi-ovoid bodyform (Text-fig. 1F,4, 5). Secondarily it led also to their later adoption of enrolment; but there is no reason to believe that any ancestor of the chelicerates enrolled, which supports the conclusion that they diverged very early from the trilobite.

For benthonic locomotion the anterior peripheral head spines would be a great hindrance, and in trilobites in general only one pair directed rearwards and at the postero-lateral angles of the head survived. In proparial trilobites (e.g., Dalmanitinae, Raw, 1925, 1927, see below Text-fig. 2B) the pair primitively in that position survived and the others aborted; and in the known ontogeny (Silurian) of *Dalmanites*, they are not seen. In mesoparial (e.g., Paradoxidae, Olenidae, etc.) the middle pair, the parial, rotated rearward, the other two pairs aborted; and in the ontogenies of Paradoxidae the procranidial is not seen though it is in some Olenidae and Dicellocephalidae (Raw, 1952, p. 854; see below Text-fig. 1,2). In metaparial (Olenellidae) the anterior as well as the middle pairs rotated to the rear (attributed to early adoption of benthonic life) so that all three pairs were crowded on the posterior border: in this family in several ontogenies all three pairs are seen; and it is interesting to note, that in the *Holmia* group (Holmiinae), judging from *H. kjerulfi* and from *Callavia callavei* (Raw, 1925, p. 303–306), the procranidial and the parial coalesced in the genal spine while the metacranidial alone forms the intergenal spine (Text-fig. 2D–4), whereas in the *Olenellus* group (Olenellinae), judging from *Elliptocephala asaphoides* and *Paedumias yorkense* (Resser & Howell, 1938, pl. 6) the metacranidial and the parial may coalesce in the intergenal spine, but the procranidial alone forms the genal spine (Text-fig. 1G, 3A–D).

The semi-ovoid body-form involved a tetarto-spheric cephalon; and its attainment entailed: in proparial trilobites, the abortion of the procranidial and the parial; in mesoparial, abortion of the procranidial and rotation of the parial; but in metaparial, rotation of both parial and procranidial, which latter forms, at least in part, the genal spine, and is followed by reduction or abortion of the others. Only one *primitive* family is metaparial, whereas several are mesoparial and several are proparial. It would appear, therefore, that the normal preparation for the benthonic life involved abortion of the procranidial spines; but that the Olenellidae arose by taking to the benthonic life abnormally early before those spines had aborted, and which consequently were rotated to the rear. The form of the protaspis also supports this view, being beautifully adapted to lie on the flat sea floor.

Polychaets usually exhibit an elongate body comprising great numbers of segments and there is strong reason to believe that the immediate ancestor of the arthropod had a great number. The evolution of the semi-ovoid body involved, therefore, great curtailment of the segmentation, for which in trilobites, chelicerates and Crustacea there is abundant evidence.

Behind the tetarto-spheric head, postcephalic segments formed the rest of the semi-ovoid. Primitively, however, the pleural body-lobes were considerably narrower than the rachis and were constituted of *separate* pleura covered below as well as above by strong cuticle. But in the development of protection the pleura extended enormously out and down till they reached the substratum. This was effected by two changes, the first being an interstitial growth be-

tween the pleura and the rachis forming secondary enlargements. These differed from the primitive pleura in being connected with their neighbors in front and behind by soft cuticle; and by being bounded below by the same, though above by strong cuticle, like that of the primitive pleura. Second, the primary free pleura lengthened greatly, and became falcate in form, with their ends curving rearward, so as to offer little resistance to forward movement. By this means the terga of rachis and pleura throughout the body came to form a semi-ovoid shield, the first postcephalic segment often fitting to the cephalon, and all behind fitting to one another; the pleura, now falcate, fitting edge to edge, to form continuous lateral walls (Raw, 1953, p. 112, 116–119, fig. 6). Barrande's figures of *Paradoxides* other than *P. bohemicus*, and Westergård's figures of the early *Paradoxides* of Sweden all illustrate this adaptation splendidly; and the primary and secondary parts of the pleura are clearly distinguishable in many, especially in convex moulds of the test (Westergård, 1936, pl.2,5,6). The writer demonstrates it for *Callavia callavei*, and Walcott's and Resser & Howell's illustrations of other Olenellidae further illustrate the adaptation in this family (Resser & Howell, 1938, pl. 3–11). It is remarkable that this striking adaptation has been overlooked by all previous writers.

The evolution of this semi-ovoid shield had at least six very striking effects.

1. It involved enormous redundance of segments, but within the trilobites the curtailment was effected in a variety of ways.

2. The evolution of the falcate pleura, all fitting perfectly to one another entailed a loss of the merocyclic specialisations of the pleura, which primitively existed; and, instead, effected the development of a perfectly graded series. This factor, more perhaps than any other, prevented the trilobites in general from being nomomeristic, in contrast with most of the higher arthropods.

3. The stable position of a semi-ovoid heavier than water when swimming or settling in water is convex-side down, and this entailed the need of organs for righting the animal, after settlement. (See 5.)

4. The habitual longitudinal arch of such a body, somewhat embedded in the mud, would, when straightened, enable the trilobite to exert a rearward push, which would effect forward advance of the head either by gliding over the sea floor or by ploughing through the mud. The front and rear of trilobites are often shaped for this function.

5. The same longitudinal arch caused the posteriorly directed axial spines to radiate in the median plane; and those towards the rear of the ovoid were directed to the sea floor. These or the longest of them, those on the macrosomites, in particular cases were developed into important organs for righting the body after swimming, or for intensifying the forward push when the longitudinal arch was straightened. In *Ellipto-cephala asaphoides* the 14th to 18th post-cephalic axial spines are all greatly developed; but in other known members of the Olenellinae it is always the 15th which is so developed, i.e., on the 5th macrosomite behind the head. But with different degrees of curtailment comparable great spines might be expected on the 12th, the 9th and even the 6th, i.e., on the 4th, 3rd and 2nd post-cephalic macrosomites. In *Callavia*, on the contrary, the thoracic axial spines form a uniform series, because in this the righting organ is the great occipital spine, which reaches a superlative development in *C. hastata* (Raw, 1936, p. 259, pl. 19, also below, fig. 4).

6. The semi-ovoid, when its defense proved insufficient, changed to the sphere very readily by enrolment, and this led to the fixation of posterior segments in a pygidium comparable in size with the opposing head or else fitting to it near the inner edge of its doublure. Several more advanced families had already reached this stage before Cambrian time. We can imagine browsers over the surface of algae rolling up and dropping down.

It was the Olenellidae that still displayed most clearly the early stages of changes 1–5, perhaps because their mode of life enabled them to remain most primitive. Regarding curtailment of segmentation, much had doubtless been effected long before Cambrian time; but the "Olenellinae" display various stages in the curtailment of the segments towards 15 post-cephalic. In the typical members of the subfamily the most important organ at the rear is the great tail-spine on the 15th segment closely comparable with the tail-spine of *Limulus*. Be-

hind the head the merocycles are in triads (very clearly seen in the little *Olenelloides*), the 3rd segment, a macrosomite, bears macropleura, and the 6th also bears larger pleura than those in front. No further traces of merocyclism in *Olenellus* can be seen till we reach segment 15 owing to change 2 (Walcott, 1910; Resser & Howell, 1938). Primarily, however, each macrosomite may be expected to have borne a macracanth and macropleura; and what we find can well have been evolved from this. Behind the 15th segment with its great median spine we have segments which are both primitive in the small size of their pleura and reduced in that the pleural furrows are missing and that the segments are shorter and are weakly sclerotised. These are followed by a small pygidium which, from its size and its character, might represent a coalescence of very few segments.

The number of these relatively undeveloped segments is at least 20 in *Olenellus robsonensis* (Burling) (Burling, 1916), 10 in *O. vermontanus* (Hall), and in *O. georgiensis* Resser & Howell, "about 4" in *O. ruddyi* Resser & Howell, 3 in *O. thompsoni* (Hall), 5 in *Paedumias yorkense* Resser & Howell, 2 in *Wanneria walcottana* (Wanner); and it may well be 0 in some *Olenellus* species.

The build of the body indicates that in the Olenellinae the 15th post-cephalic was the last important segment, and that those behind were undergoing reduction. In the writer's view the spine is homologous with that which terminates the body in the eurypterids, and with the scorpion's sting, as discussed below. It is serially homologous too with the tail-spine of Aglaspida which is on the 12th, and with the tail-spine of *Limulus* which is on the 9th post-cephalic and therefore, again the macracanths of macrosomites, as discussed below. In the scorpion and eurypterids as well as in *Limulus* the anus opens beneath the tail-spine. Did it already do so in *Olenellus robsonensis* in front of its 20-plus posterior reduced segments, and likewise in the other *Olenellus* species? It seems very probable indeed that it did, and that also through the whole range of the chelicerates the anus is a secondary opening!

Whatever may be the answer to this question, comparisons with *Olenellus* and other trilobites proves conclusively that arachnologists are wrong in regarding the tail spine in chelicerates as either (1) a coalescence of several segments (Fage 1949, p. 221); or (2) as the equivalent of a flagellum (Millot, 1949, p. 536 and Petrunkevitch, 1948A); or (3) as a telson, i.e., the homologue of the terminal part of the body of the annelid (Millot and Petrunkevitch). The tail spine in *Olenellus* is so closely comparable with like organs in xiphosures, eurypterids and scorpions that all workers would accept them as at least serially homologous. And the organ in *Olenellus*, as comparisons prove, is a development of a single axial spine on a single segment, i.e., a development of a primitive segmental organ inherited from the pro-arthropod and possibly from the polychaet (Raw, 1953, p. 84,120,121). Such a spine, has not been seen on the anal "segment"; and in *Olenellus* the spine is often far removed from the primitive telson or analite, and in origin had nothing whatever to do with it. For this reason, where, as in so many chelicerates, the anus is closely associated with a spine, it is probably secondary; and does not imply the existence of the telson. This word indeed has been so misused that, without definition each time, it is useless. The writer would suggest that it be replaced by analite.

The structure of the trilobite pygidium is of significance for the mode of curtailment. In *Wanneria walcottana*, which has a large axial spine on the 15th post-cephalic segment and two free segments behind this, the end of the body consists apparently of a single segment bearing a single pair of pleura which are directed rearward, their posterior edges being apposed to one another along the mid-dorsal line. This segment is besides the 18th post-cephalic a macrosomite; so here not only was the 15th post-cephalic an important segment bearing the greatest median spine but the 18th was also important bearing the last important pleura, behind which all the remaining segments had aborted (Walcott, 1910, p. 30, fig. 8,10,12; Resser & Howell, 1938, pl. 11). A similar termination, but with much longer pleura was figured and described by the writer as *Wanneria? pennapyga* (Raw, 1936, pl. 21, fig. 3a–c).

In such cases, where we have a definite normal segment at the rear instead of a col-

lection of underdeveloped segments, the suggestion offers itself that the anal and reduced segments may have been discarded and that here again a new anus may have arisen.

In *Callavia*, too, within the *Holmia* group (the Holmiinae), the small end-piece is apparently a single segment bearing a small median spine, behind which is presented a single pair of pleura united in the mid-line belonging to the same segment. It is apparently here the 19th post-cephalic segment (Walcott, 1891, p. 639, pl. 91; Raw, 1936, pl. 18, fig. 16; pl. 19, fig. 6; pl. 23, fig. 3,16). In *Holmia*, which belongs to the same subfamily, it appears probable that the segmentation is the same; for there are 16 free segments, and the terminal member is here a pygidium in which "the short axis, which is rounded posteriorly, shows a faint bipartition or tripartition" (Kiaer, 1916, p. 63).

For the body functions not more than about 15 or 18 post-cephalic segments seem to have been needed; for in this family when this number is exceeded, the posterior segments are reduced and the long pleura in front fit round the short pleura behind forming thus a continuous posterior wall of the semi-ovoid, as seen in *Nevadia weeksi* Walcott, *Olenellus* and *Paedumias*, and *Elliptocephala* (see Text-fig. 5). In *Paradoxides* too the effective segments are about the same in number. According to Westergård (1936, p. 40) the most primitive, *P. torelli* Holm, has 21 free segments and others in the same lowest *Paradoxides* zone of Sweden have down to 17 (p. 33,41). All exhibit the adaptation to the semi-ovoid body-form (Text-fig. 1F). But in this family we never have a number of reduced free segments at the rear. Particular species in both families departed from the semi-ovoid form, reverting towards the larval character, namely, *Olenellus vermontanus* (Text-fig. 1G) and *Olenellus georgiensis* which may be the two sexes of the same species, *Olenelloides armatus* (Text-fig. 1C) and *Holmia kjerulfi* in the first family and *Paradoxides bohemicus* in the second.

The segments immediately in front of the anus were apparently less completely functional than the rest and in *Holmia* two have joined up in the pygidium; in *Paradoxides*, too, a few seem in all cases to have done so. One cannot avoid the conclusion that it was the semi-ovoid that determined the number of post-cephalic segments.

That merocyclism was lost in the evolution of the trilobites is abundantly suggested by the ontogenies, as the writer stressed as early as 1924. In Olenellidae, Paradoxidae and Olenidae the head spines are usually reduced in the ontogenies to one pair. In *Elliptocephala* the 3rd thoracic is macropleural in the larva, not in the adult; and in paradoxides the 2nd thoracic is macropleural in the larva, when not in the adult.

That the evolution of the semi-ovoid form would determine the position of stability for swimming is self-evident; but it is also supported by the swimming of the larval *Limulus;* and as in this the tail spine when developed is of use for righting the animal on settlement, so was this probably the case in the Ollenellinae (*Olenellus* and *Wanneria*); or the group of posterior spines in *Elliptocephala*, *Holmia* and *Kjerulfia* might be used, or even the occipital head spine of *Callavia*.

The longitudinal arching entailed by the semi-ovoid was not always in the Olenellidae uniform throughout the body, though practically so in *Callavia* and *Kjerulfia*. The use of the rear segments as a whole and especially the use of axial spines led usually to the rear segments descending more steeply, and not improbably there would develop a point of more rapid change which would mark a difference of function—the segments in front, high, and functioning in clearer water for respiration, the posterior, descending, reduced segments, in muddier water, much less important for this function, but in *Elliptocephala*, *Holmia* and *Kjerulfia* developing a series of posterior axial spines though in *Olenellus* and its relatives only that of the 15th post-cephalic as a great spine.

Since the writer believes that ancestors of the Olenellidae gave origin to the chelicerates it is important to consider the status and mode of life of that family; and since they were marine, we can help ourselves to some degree by suggestions from their modern marine representative, the king crab.

The Olenellidae were trilobites and, as claimed by the writer, the segmentation of their cephalon corresponds exactly with the prosoma of the chelicerate. They are peculiar only in having lost from the cephalon the facial sutures along which in the majority of families the head shield split in ecdysis. Here these are replaced as the ecdysial parting by a sub-marginal suture, which is completely explicable as a result of the migration of the procranidial spines and neighboring parts round to the genal angles, whereby the rostral suture with the connecting sutures at its ends became a great sub-marginal semicircle (Raw 1924, p. 101; 1925, p. 305, 311, 312; 1937). This is probably the origin also of the marginal suture in some other trilobites, but probably because they were post-Cambrian and less primitive, it has not yet been proved. It can still be seen as the sub-marginal ecdysial suture of the king crab.

The trilobite appendages.—Under the head *Olenellus* bore a pair of antennae as discovered by Dunbar in *Olenellus getzi* projecting beyond the cephalic shield (Dunbar, 1925, p. 303, fig. 1,2; Resser & Howell 1938, p. 221, pl. 5, fig. 2). Unfortunately we know nothing of their other appendages apart from the pleura, which, though appendages in origin, are greatly modified and coalesced on the cephalon so as to form the cheeks; though behind the head as the pleural "spines" they maintain their character as free appendages and were moved by muscles, fitting together perfectly so as to form the lateral and posterior walls of the semi-ovoid. There is, however, every reason to believe that they bore normal trilobite appendages.

In the earliest of the known chelicerates, the merostome order Aglaspida of the Upper Cambrian and the order Beckwithida represented by a single form from the Middle Cambrian (*Beckwithia typa* Resser) the pleura are still very large and functionally important. They are here closely comparable with those of olenellids, and their function was still the same, namely, the maintenance of the semiovoid body-form (Resser, 1931; Raasch 1939). In *Aglaspis spinifer* their form is falcate, like those of *Callavia* and *Kjerulfia* (Text-fig. 9A); but they grade into the rachis instead of being abruptly separated from it by dorsal furrows. In the Aglaspida the body ends in a great axial spine which is identified with the 12th post-cephalic segment. In *Beckwithia* the tail spine is on the 9th.

In the order Eurypterida the pleura throughout the body are reduced, but specialisation affects them differently in the pre- and in the post-abdomen and very differently in different families. Usually the passage dorsally into the rachis is a perfect gradation. In *Mixopteris kiaeri* Størmer, however, dorsal furrows exist in the pre-abdomen and may be regarded as inherited (Størmer, 1934, p. 112, pl. 5). In *Dolichopterus macrocheirus* Hall and in *Anthraconectes* pleural spines are still conspicuous in the post-abdomen. The great development of the pleura, which in the trilobite went with the semi-ovoid body-form, connoted a soft ventrum. The reduction of the pleura in the chelicerate is accompanied not only by a loss of the semi-ovoid but also by the strengthening of the ventrum so that its post-cephalic part is quite comparable in strength with the dorsum. On the whole the greatest reduction of pleura occurs in the most active forms like *Hughmilleria* and *Pterygotus*.

Though of ventral appendages only the antennae have as yet been discovered in the olenellids, from the close comparisons which can be instituted with other trilobites, there can be no doubt whatever but that all the normal segments including those of the head bore normal trilobite ambulatory-respiratory appendages; and of the forms of which the appendages are known, those of *Neolenus serratus*, both from its nearer relationship and from its antiquity, will best serve as guide (Walcott, 1921). The appendages of trilobites have been the subject of much controversy, for which there is here no room. It is agreed that (omitting the pleura) they are biramous and that they consist of a walking branch comparable with the walking limbs of other arthropods and of a respiratory and natatory branch which has been compared both with the exopodite of Crustacea and with the gill-bearing organs of chelicerates. Størmer has given the latest description of the appendages and has demonstrated that the setae borne by the gill branch have the

form of blades. But he has claimed that there is no homology between the gill branch of the trilobite and the exopodite of the crustacean (1939). The writer on the other hand has claimed that the appendages even in the pro-arthropod were already biramous (1953, 2, p. 83,84), which implies the probability of that homology, which is the expressed view of Calman. Here the matter can be left as we are not here concerned with other arthropods.

Whatever the truth may be, it will doubtless be agreed with Størmer that the trilobite appendages are homologous with those of the chelicerate; that the walking branch of the first is homologous with the walking leg of the other; and that the gill branch is homologous with the gill branch of the xiphosure and eurypterid, and the blade-like setae with their gill-plates and with the lung sheets of arachnida.

The trilobite limbs ancestral to those of the arachnid were of similar character throughout the whole body over both the head and the post-cephalic body. In contrast, in the arachnid we have on the head the representation of the walking branch (the arachnid walks on its head) and in the body the respiratory branch, and this very meagrely except that we still see the walking branch in greatly reduced and modified form throughout the abdominal appendages in the xiphosure, and in the eurypterids only in the genital organs.

The eyes.—Of other external organs passed on by the trilobite the most important are the eyes. The origin of the eyes of trilobites and of other arthropods has been discussed by the writer (Raw, 1953). All except the compound eye were inherited from the polychaet. Those of the polychaet are all, in origin, segmental eyes, a pair properly belonging to each segment of its ancestor. The prostomium had acquired two pairs, a pair with each of two out of the three pairs of ganglia of the mid-brain which in the evolution of the brain had been added to the fore-brain (Raw, 1949, p. 19–22). These form in the arthropod, Class I. The peristome, though not a normal segment is deduced to have borne a pair of eyes which became Class II. The following six segments each contributed a pair, Class III. The compound eyes, evolved in the arthropod, constitute Class IV.

In their head or prosoma Chelicerata are much the most primitive of modern arthropods and *Limulus* is in all respects much the most primitive existing form. Accordingly, in its ontogeny all four classes of eyes are fully represented, though in the adult only classes I and IV are present as visual organs. This being so, it is remarkable that only classes II and IV are known to exist in the olenellid trilobites. This again suggests the antiquity of the chelicerate and the trilobite already in Cambrian time. However, it is probable that all the eye classes were represented in the olenellid ontogeny, as well as in their phylogeny.

In Olenellidae the only dorsal eyes known are compound. The structure of the eyes is best exhibited, so far as the writer is aware, by *Holmia kjerulfi* and *Kjerulfia lata* described by Kiaer (1916), but no research on them has as yet been prosecuted. What we have is naturally limited to the external cuticle.

The first discovery of the visual surface of such eyes was claimed by Walcott (1910, p. 239, p. 43, fig. 5,6) who discovered the visual area in a young cephalon of *Olenellus gilberti*, 1.6 mm. long. Walcott says

> In one species I have been so fortunate as to find the outer facetted surface preserved. This surface is perforated by minute rounded hexagonal openings arranged in . . . more or less quincunx order. The interstitial spaces between the openings are narrow rounded ridges. There is no trace of a corneal covering and the surface is so much like that of the outer surface of the eye of *Limulus* that I cannot avoid the conclusion that they are of the same type . . . and inward projections of the outer cuticle, Bernard 1894, p. 422.

One may comment, however, that the minute specimen in question only 1.6 mm. long and exhibiting three pairs of peripheral spines could only have been exposed if the test had been dissolved away causing the shale to split just there. Besides Walcott himself says "there is no trace of a corneal covering." Hence it is very probable that Walcott was not looking at the external surface of the eye, but at the surface of an internal mold of the test, i.e., molded upon the internal surface of the cornea.

Kiaer was the first to adequately figure and describe the eyes in adult olenellids, though Walcott had figured the eyes in imperfect specimens of *Olenellus gilberti* (1910,

pl. 36, fig. 4a; pl. 43, fig. 5,6) and in *Callavia callavei* on a specimen supplied by Raw (1910, pl. 42, fig. 2). Lindström (1901) had claimed that both Olenellidae and Paradoxidae were without lateral eyes, the palpebral lobes having only a crescentic slit beneath them, the condition they present when collapsed in shale. But when preserved in sandstone or limestone in both families the area of the visual surface is seen, even if this surface is not preserved. Kiaer describes the area in *Holmia kjerulfi* (1916, p. 61,65) and figures it (p. 61, pl. 7, fig. 1–3). He says

> the optic membrane has almost always disappeared, and the palpebral lobe is pressed down so that only a crescent-shaped fissure remains. The eye itself which was found in an excellent state of preservation in two specimens is quite low and especially in front narrows somewhat at the ends.

Again (p. 65)

> The surface itself is well preserved at several places and consists of quite fine, hexagonal, smooth facets.

Comparing his observation with that of Walcott, he concludes that the latter's "specimen must have been defective." Kiaer also figures the eye of *Kjerulfia lata* Kiaer with a similar character and preservation (pl. 12, fig. 3). The writer, too, when examining the specimens from Tömtem, Norway in the University Geological Museum at Oslo was surprised to see that both these species preserved the eyes, and that a ×10 lens only just resolved their compound character. How ancient already in the Lower Cambrian must the compound eye have been! Each eye is a large crescent in plan embracing half a circle with a length of about four head segments and with the visual surface gently arched across its length. This, however, was delicate, and is usually represented in the fossils by a blank space.

Excepting the Pantopoda which are aberrant, one may note that the aquatic chelicerates (the Eurypterida, Aglaspida and Xiphosura, which are claimed below as having respectively 15, 12 and 9 post-cephalic somites) are furnished with compound as well as simple eyes, whereas the terrestrial chelicerates without exception have only simple eyes. Both compound and simple eyes indeed, all classes I–IV—must have been inherited from the pre-Cambrian trilobite ancestor.

Ventrally near the rear of the trilobite hypostome were a pair of "maculae" which in the families Paradoxidae and Olenellidae are represented by holes through the test. They were figured and described by Lindström (1901) throughout the other families of trilobites and from their structure were claimed as eyes. Not all workers have accepted them as such but they are believed by Hanström, Størmer and the writer to be eyes, homologous with the "ventral eyes" of the *Limulus* larva. These are made class II by the writer and are deduced to have migrated from the rostrum on to the hypostome after the prostomial eyes, class I, had migrated on to the dorsal side where they are seen, for example, in *Limulus* as the median eyes (Raw, 1953, p. 93,97–103).

Two of the four classes of eyes claimed as primitive in arthropods are not recognised in the Olenellidae, namely, the Prostomial Class I and the Metastomial Class III; though both of these are represented in chelicerates, Class III, e.g., as the lateral eyes of the scorpion and the vestigial eyes submerged under the compound eye of *Limulus*. The writer would, however, claim the presence of metastomial eyes in a related trilobite family, the Phacopidae, namely in *Phacops latifrons*. And it is not improbable that both classes of eyes would still be represented in the embryology of the Olenellidae. It is indeed not improbable that some of the eyes missing from the Olenellidae were actually present in the adult. Thus *Nevadella burri* (Walcott) bears a "tubercle" between the palpebral lobe and the glabella, which may be a residue of the Class III eyes (Walcott 1910, p. 280 and pl. 28; Raw, 1936, p. 280). In the holometabolous insects the metastomial eyes Class III of the larva and some times the Class II eyes are replaced by the compound eye Class IV in the adult. Examples are Lepidoptera, Coleoptera and Diptera.

Special importance of merocyclism for the chelicerate.—Study of the subfamily Olenellinae has shown how a metaparial trilobite with merocyclism of its particular type gave rise to an *Olenellus* with 15 post-cephalic significant segments and with varying numbers of greatly reduced segments beyond the 15th, which in contrast with all the other

segments is specialised by great development of its axial spine. This evolution would seem to have been determined by their early adoption of the benthonic life and controlled by their close apposition to the sea floor, through which they shallowly burrowed and which caused them to develop the semi-ovoid body form. Exactly the same kind of evolution is believed to be behind the Eurypterida and the Scorpionida.

But where the evolution of shorter bodied forms was favoured the same merocyclism gave rise to forms with 12 or 9 or 6 significant segments, the remainder behind being either reduced or lost, as is the case in other Chelicerata, e.g., Aglaspida with 12, *Limulus* with 9 and some Acarina with 6.

Just as the Olenellidae exhibit a few marked reversions from the semi-ovoid form, so *Limulus* has departed completely from this form. But, that its ancestor had had it, is suggested by the great development of its tail spine, analogous and serially homologous with that of the Olenellinae which in origin is clearly associated with the evolution of this form. Both are developments of the axial spines of macrosomites: the fact that one is on the 15th and the other on the 9th suggests that the ancestors of *Limulus* departed from the trilobite long before the Cambrian period by which time the 9th segment had quite lost its specialisation in almost all known olenellids. This conclusion is further supported by the fact that still other chelicerates have 12 and others again have only 6 significant segments behind the cephalon.

In the Olenellidae the dominant build is a beautiful adaptation to the semi-ovoid form. This is seen in the genera *Olenellus* (e.g., *O. thompsoni*), *Wanneria* (*W. walcottana*), *Paedumias* (*P. yorkense*), *Elliptocephala* (*F. asaphoides*), *Callavia* (*C. brōggeri*), *Kjerulfia* (*K. lata*) and *Nevadia* (*W. weeksi*). In all these mentioned the pleura are beautifully falcate, whereas the primitive form judging from early larvae and many primitive adult genera was short, parallel sided and abruptly and obliquely terminated along the direction of the pleural spines (Walcott, 1910; Resser & Howell, 1938).

At the rear, however, there is some modification of the ovoid. In *Elliptocephala* the posterior five segments (14th–18th post-cephalic) with great axial spines are bent down rearward more steeply, and the long pleura of the segments in front fit round the short pleura of these segments. This is an adaptation to the use of their axial spines which are so graded that all would together engage the sea floor (Text-fig. 5A).

In *Olenellus* and *Paedumias* one spine only, the 15th post-cephalic, is developed; behind which the long pleura of the segments in front fit against the greatly reduced segments behind (Text-fig. 3,5B).

In *Nevadia weeksi* the pleura back to the 17th are long and falcate, in life fitting perfectly to one another and against the last dozen segments which are much reduced. The axial spines have in this genus aborted (Text-fig. 5C).

These posterior modifications of the ovoid body form subserved two functions, namely, propulsion of the body through the mud, or the righting of the body after swimming, or both of these.

The semicircular eyes with vision all round suggest relatively stationary habits. Their position, well elevated, near the glabella and well away from the head margin and their level base suggest that the creature may have been habitually buried up to the eyes in mud. But the build of the body behind, adapted, the writer thinks, for pushing, combined with the above mentioned features suggest that they repeatedly ploughed forward through it. If, when they did so, they lowered the head they would clear a space in front for the entrance of water, which, during the stationary period, by the motion of the gills could be made to issue at the rear.

The primitive nature of the Olenellidae is indicated by the following morphological features: the clear segmentation of the cephalic rachis, the retention of diadic merocyclism in the cephalic spines, the simple post-cephalic segmentation, the large number of segments, the small pygidium or its absence, and the marked vestiges of triadic merocyclism in this region notwithstanding that the life of the trilobite tended to suppress it. These indications of primitive character are supported by its antiquity, and the delicate nature of the exoskeleton. Only a primitive family could be expected to give rise to another class of arthropod.

This family also conclusively indicates for

the chelicerates: (1) the morphological significance of the tail spine, as representing a single segment; (2) that where such is present (and probably also in all other chelicerates) the anus is a secondary opening; (3) that there is no functional telson; and (4) that the flagellum of the related Arachnida, where it exists, is a series of reduced segments.

That early members of this primitive family and no other gave rise to the chelicerates is suggested by the following facts.

1. The Olenellidae is the only known primitive family which was metaparial, and in consequence had lost the dorsal facial sutures; and the earliest of known chelicerates closely resemble them and show no trace of these sutures.

2. In this family these sutures have been replaced for ecdysis by the crescentic submarginal suture (the coalesced rostral and connecting sutures), which closely corresponds both in position and function with that of *Limulus* and of some other Merostomes.

3. Only this family retained for so long the primitive triadic merocyclism behind the cephalon, without which no family could be expected to give rise to forms with 15, 12, 9 or 6 of important post-cephalic segments.

4. This family alone is known to have evolved post-cephalic tagmata and organs both analogous and homologous with those of chelicerates.

5. It also interprets for us: (a) the tail spine as originally the axial spine of a normal segment, and therefore *not* a telson; (b) the unique chelicerate anus as a secondary opening; (c) the post-cephalic tagmata as controlled by merocyclism; and (d) the flagellum as a series of reduced normal segments.

6. The Olenellidae, indeed, enable us to picture the evolution of the subphylum.

Seeing however that already in the Lower Cambrian the Olenellidae had largely lost their merocyclism from the post-cephalic body except for the 3rd and 6th which show it only in the pleura and the 15th which shows it in the axial spine, the origin of the chelicerates from the Olenellidae was very long before Cambrian time. This, too, is amply supported by the paleontological record which has furnished merostomes from the Cambrian, scorpions from the Silurian and even mites besides other arachnids from the Old Red Sandstone.

4. ORIGIN OF THE CHELICERATES, IN OUTLINE

The supposed way in which the chelicerates originated may now be sketched. We can omit the Pantopoda from our survey for the present as presenting too much difficulty, and can limit consideration to the Merostomata and the "Arachnida." The value of the olenellid trilobites for the interpretation of both these classes indicates that all have a common ancestor from which the divergence of the chelicerates is attributed to change of habitat.

The Olenellidae were marine and inhabited the sea floor of northern coastal seas in Cambrian time, being found in the Lower Cambrian on both sides of the north Atlantic between the Rockies and Siberia. They burrowed through the surface of the mud and silt and silty sand, and we must assume that the common ancestor of this family and of the chelicerates did the same.

The Merostomata inhabited the same region, their earliest known forms coming from the (Middle and) Upper Cambrian of north-central and central U.S.A., the Ordovician of New York and other states, and from the Silurian to the Carboniferous of Europe as well as North America. In contrast with the trilobite there is good reason to believe that the Merostomata were predominantly and perhaps entirely freshwater creatures except for the Permian to Recent limulids (O'Connel, 1916); and it is probable that all the Arachnida had aquatic freshwater ancestors.

The divergence of the chelicerates from the marine ancestor of the olenellid can be attributed to the discovery of the river estuaries, where they found both food and security, and where their burrowing habits prepared them to resist the twice daily scour of the tide. Here also they became inured to the change of salinity in the water; and in proportion as they succeeded in these two respects they would be enabled to spread up the rivers into perfectly fresh water, where perhaps there was still greater security from predators. Burrowing also enabled them to resist the stress of the increasingly rapid flow of the water. In this way they ascended the rivers, and reached the lakes within

which there would be new opportunities for deployment, and from which they invaded the land. Judging by their modern relatives and their deduced body-form and habitat, their food was animal, perhaps chiefly worms of various kinds, but also all that could be mastered, and which had preceded them up the rivers and their beds.

Several different rivers would debouch in the marine habitat of the ancestral olenellids, and hence different forms would be evolved in different river basins, and different conditions would be experienced also in different tributary basins; for, owing to geological causes and the separation of river basins, these habitats would differ much more in water composition and temperature, and so in life, than would the ocean waters at the river mouths.

This ancestor was already a trilobite, furnished with compound eyes (Class IV), which in the ontogeny superseded in function the six segmental metastomial eyes (Class III), also with the single pair of "peristomial" eyes Class II and the two pairs of "prostomial" eyes (Class I). These last had probably early migrated on to the dorsum, whereas the Class II eyes may have migrated on to the labrum, as in trilobites. It still had extensive merocyclism, exhibited especially in the size of pleural and axial spines on the macrosomites. Probably it was already metaparial like the Olenellidae. Its appendages were (on all segments throughout the postcephalic body) a pair of pleura, which were still moved by muscles, those on the head having coalesced into the cheeks in the origin of the arthropod. On the rostral "segment" were a pair of antennae, and on all the normal segments were biramous appendages of which six were on the head. As in the Olenellidae various scions had developed the semi-ovoid body-form, which was well adapted to the burrowing mode of life, necessitated by the new habitats. Evidence exists for the belief that owing to the merocyclism, in some as in *Olenellus*, the semi-ovoid body utilised 15 post-cephalic segments, whereas others used smaller numbers. Seeing that the creatures on which carnivorous forms could subsist were of all sizes from unicellular organisms up, we can imagine the application of merocyclism to the origin of smaller forms with 12, 9, 6, 3 or even 0 significant abdominal segments. Thus, given merocyclism, there is no inherent difficulty in imagining the origin of the ancestor of the Acari, or even, given also a return to the sea, of the origin of the Pantopoda. Behind the significant segments the remainder were greatly reduced or aborted.

Owing to their mode of life (largely stationary, and half buried in the mud necessary for maintaining position against the currents, and with slow locomotion of ploughing through the mud) it was of advantage for them to be smooth, so as not to give enemies and water currents a purchase, hence in place of the deep axial furrows of the trilobite they developed an almost evenly arched transverse profile and a smooth body surface.

Also, because of this mode of life the antennae were lost through disuse, and the labrum was reduced. The first normal pair of appendages already reduced became specialized for the holding of food and became the chelicerae; the other five belonging to the head specialised mainly in the gathering of food as well as in locomotion by pulling, levering and pushing. Consequently on all these the gill branch was reduced. But, judging from *Limulus* and the Eurypterida, the coxae of all these five cephalic pairs served the mouth by lacerating the food.

Behind the head the appendages developed other functions. The first pair moved forward to close the rear of the food groove between the cephalic coxae. The function developed by those behind resulted from the arching of the body and the burrowing mode of life. The highest part of the arch immediately behind the head had the clearest water beneath it, and formed a hydropome or water-bell. The second postcephalic pair of appendages came to specialize in the genital function, though this previously would be spread through the body segments. The limitation of this function to this segment would be gradually acquired, and its situation is probably closely connected with the limitation of the endopods with locomotory function to the segments in front. The succeeding pairs of appendages still in the clearest water (to the number of five at least in some) specialised in respiration, gradually lost their ambulatory function, and so lost their endopods.

This was because the function of these in locomotion, except for swimming, was taken over by the use of the dorsal surface of the body behind, i.e., the axial lobe and pleura and sometimes a posterior axial spine. All these united in exerting a rearward push when the body arch straightened, their action being supplemented by use of the cephalic limbs. This consideration fully explains also the entire loss of appendages other than the pleura from the posterior part of the body which was in mud and muddier water. It explains also the absence of ambulatory endopods from the anterior abdominal segments. The habitual attitude of the evolving chelicerate was facing up-stream: the natural flow of the river carried water in under the front of the head shield, and by motion of the gill-bearing appendages it was driven rearward to escape behind. It was natural for them to progress mainly upstream and so they attained the lakes.

This loss of ambulatory function in the appendages throughout the whole post-cephalic body, while it was well adapted to aquatic life, constituted a terrible and unique handicap to those chelicerates that crawled out into the air, and the handicap was the greater the longer was the abdomen. Of those with 15 abdominal somites only the scorpions survive to our day. This handicap was unique among the terrestrial fauna: even the vertebrates had the two pairs of fins from which to evolve their legs. The slow locomotion that it immediately entailed led to the loss of compound eyes, to the stalking of their prey and even to cannibalism between mates.

The great variety exhibited by the subphylum is explicable. To the variations in the environment and food was added both merocyclism and the development of the semi-ovoid body-form. To these and other factors are attributable the various numbers of significant postcephalic segments (15, 12, 9 and 6), also the presence of tail spine or flagellum, the former a development of an axial spine of a normal segment, the latter a development from a succession of such segments greatly reduced. All these are explained by what the Olenellidae exhibit.

It was claimed by G. H. Carpenter that, as suggested by Malacostraca and insects, the primitive arthropod was nomomeristic and he claimed as evidence that *Olenellus* had the same limited number of segments; but he was not a specialist in the trilobites, and he quite missed the significance of the family to which it belongs.

The curtailment of segmentation in the chelicerate had not only different effects from those in other arthropod subphyla; it was also different in nature. In all chelicerates it would appear probable that the anus is a secondary opening into the alimentary canal, and that there is no representative of the telson. There is good reason also to believe that the same was true for several genera of Olenellidae. The same is suggested also by the internal anatomy of modern chelicerates. The mid-gut is very long; the fore-gut is very short and the hind-gut is practically non-existent. Comparison with the trilobite and other arthropods explains this. Of the head appendages only the antennae are lost and six pairs survive, whereas in the other classes only 2, 3 or 4 pairs homologous with these 6 survive, though they retain antennae (or antennules). The lost appendages were incorporated in the alimentary canal and the stomodeum was extended. In *Olenellus* the greatly reduced segments behind the tail spine number in different cases between 3 and 30; and it is extremely probable that the anus was beneath the tail spine as in *Limulus* and the scorpion, and was secondary. If so, there would be no hind gut.

The Olenellidae are anomomeristic, ranging in number of post-cephalic segments in known forms from 44 to 7, but it demonstrates the origin of nomomerism, and some species of *Olenellus* seem to have reached the stage with only 15 post-cephalic segments. The Chelicerata is a subphylum remarkable in that its classes are nomomeristic but with different numbers of segments in the different "classes" as, for this reason, they might well be called.

Seeing that it is quite impossible to arrange the various classes phylogenetically, in the survey that follows they are grouped according to the supposed numbers of significant post-cephalic somites.

Petrunkevitch believes that all "arachnids" had originally the same number (12) of post-cephalic normal segments but strong evidence is here advanced against this. Sub-

sequent changes have largely masked the detailed primitive segmentation. Trilobites are so primitive that the segmentation is perfectly clear from the terga alone, except in the extreme front of the head and in the extreme rear, the former due to the presence of the labrum underneath and the latter due to curtailment causing degeneration of posterior segments. In the earliest and most primitive chelicerates, too (the Cambrian Aglaspida), the segmentation can hardly be doubted; but in modern forms, thanks to embryology, it is clear that the 1st abdominal tergite is lost in many, owing to the change of position of the pre-genital appendages at this important junction. Also, according to the writer as explained below, the last significant segment before the tail spine, where this occurs, is in some coalesced with that of the segment in front owing to the extension of the tail spine muscles. This last is a change analogous to what took place in the evolution of the Eu-Malacostraca.

Study of the Olenellidae has shown how supremely important for the evolution of nomomerism in the chelicerates was the triadic merocyclism behind the head of the primitive trilobite; and comparative studies of the arthropods shows that it was the presence of the same in the deut-arthropod that was responsible for the nomomerism of the Insecta and Malacostraca. It has already been seen that the mode of life of the trilobite tended to its complete loss, and that, omitting the aberrant *Olenelloides*, the *known* olenellids, in which alone it is seen, could not have given rise to nomomeristic forms with less than 15 postcephalic segments. The chelicerates must accordingly have arisen in pre-Cambrian time. There is reason, too, to believe that both Crustacea and insects had a like early origin.

Except perhaps for the Pantopoda, the aquatic chelicerates throughout Paleozoic time were all freshwater forms in harmony with the evolution here sketched. But in the Permo-Trias, when inland waters in Europe and North America became saline through aridity, the ancestors of *Limulus* became adapted to such salinity, and hence in the geographical changes that brought the sea into those basins they were not exterminated but became marine. Thus after some hundreds of millions of years they returned to the habitat of their pre-Cambrian trilobite ancestors and they still survive (Stromer v. Reichenbach, 1907). From the Paleozoic (if not pre-Cambrian) lacustrine waters, chelicerates in considerable variety invaded the land. This had occurred at least by the Silurian and probably very much earlier.

Summary.—The chelicerates derive from the pre-Cambrian ancestor of the ancient Cambrian trilobites, the Olenellidae, with semi-ovoid body-form. To this origin is due the absence of analite or telson and hind gut, and the presence of a secondary anus. The evolution is attributed to a change of habitat from the sea floor to that of fresh water rivers, and then to lakes. All the other characteristics that they have in common are by this explicable, including: lack of antennae; retention of all the six post-antennal pairs of appendages on the head (or prosoma), which equals the heads of other arthropods; loss of all ambulatory function from the abdominal appendages; reduction and forward advance of the 1st abdominal appendages to beneath the head, and reduction or loss of the tergite of the segment; anterior position of the genital segment; limitation of gills (or corresponding organs) to the anterior segments of the abdomen; great variation in the number of abdominal segments; and, lastly, the frequent occurrence of a post-anal tail spine or a flagellum.

5. CHELICERATES PRIMARILY WITH 15 POSTCEPHALIC OR ABDOMINAL SOMITES

Text-fig. 7,8

Introduction.—In this division, as claimed above, are included the Eurypterida and the Scorpionida.

The latter are the most primitive of modern "Arachnids" and the Eurypterida were also primitive. But the interpretations of both groups are greatly aided by the most primitive of modern chelicerates, the limulids.

That the eurypterids and scorpions are rather closely related is strongly suggested by the following morphological agreements:

1. Their equivalent cephala.

2. The comparison of the tail spine of eurypterids with the sting of the scorpion.

3. The same number of separate terga in front of the last named.

4. Identical early history of the pre-genital segment (discussed below).

5. Identical number of appendages behind the genital segments (discussed below).

6. Close correspondence in details of form between the specialised eurypterids [*Carcinosoma* and *Mixopteris* (Carcinosomidae, Størmer, 1934)] and the scorpions.

The eurypterid is the more primitive—

1. In its metastoma, which Lankester, Vachon and the writer homologise with the pre-genital "sternite" of the scorpion, but which in both cases is a coalesced pair of greatly modified appendages, but was more primitive in the eurypterids in being still functional (see below).

2. In its aquatic respiration and the greater freedom and active movement of the post-cephalic appendages.

3. In its retention of compound eyes.

4. In the character of its metastoma.

But in the pectines, the first post-genital pair of appendages, the scorpion presents us with a much more primitive form of these, still comparable with the gill branch of the trilobite appendages. This is perhaps attributable to their use in copulation. The contrast presented by these appendages in the two groups indicates how very far back was the primary divergence between them, very much earlier than the earliest known forms of each.

The so-called "sternum" or "sternite" between the coxae of the last two pairs of legs is regarded by Petrunkevitch and by Kästner as the sternum of the last two cephalic segments. The former, while recognising the chilaria of *Limulus* as a pair of appendages, states that they have no representative in the Arachnida. But they are quite clearly the equivalent of the eurypterid metastoma and the metastoma is the equivalent of the scorpion's sternum, which, therefore, is wrongly named. That this is the case is indicated by the two facts (1) that it is usually traversed by a median subdivision, and (2) that it is not depressed below the coxae on either side but up at their level. It was Lankester who first claimed that the "sternum" of the Scorpion was the equivalent of the chilaria, but he did not accept either as appendages!

The Eurypterida occur fairly frequently as freshwater fossils in countries bordering the North Atlantic from the Ordovician (U.S.A.) to the Carboniferous; and one genus *Tolypterus*, related to *Eurypterus* itself, extends into the Permian. None occur in Mesozoic rocks. Scorpions, however, known from the Silurian, range to the present day as a remarkably persistent type. It is curious that, as the writer claims below, the body tagmata correspond exactly with those of the Malacostraca, whose head, thorax and abdomen correspond in segmentation with the prosoma, pre-abdomen and post-abdomen of the scorpion. In both cases it points back to the merocyclism of the deut-arthropod.

Equivalence of all post-cephalic terga in these two orders.—In both groups 12 closely comparable terga separate the cephalon from the tail spine or sting; but this notwithstanding, considerable differences of segmentation have been supposed to exist between them.

Holm (1898) following Schmidt (1883) and many others regarded the tail spine of the eurypterid as a telson or analite behind 12 abdominal segments; and before his time, zoologists had attributed to the scorpion the same segmentation and tagmatism.

The discovery by Brauer (1894–5) of the evanescent pre-genital somite with its appendages gave the scorpion 13 post-cephalic somites in front of the sting! This was one too many for some arachnologists: Buxton (1917) pointed out that the last segment of the pre-abdomen appeared to be without a ganglion; and put forward the suggestion that

> the last pre-abdominal and the first post-abdominal represent a single segment, which has become divided into two in order to give to the base of the tail greater strength.

Petrunkevitch, too (1922, p. 180), states

> There is in the adult scorpion an abdominal segment in excess of the neuromeres . . . . I have no doubt that it is the first post-abdominal or caudal which may have subdivided into two distinct sclerite rings without corresponding subdivision of other structures.

This is supplemented (1949a, p. 126) by

> the tergite of the first abdominal somite persists in the extinct Protoscorpiones. . . . The normal number of abdominal segments is restored by sub-segmentation of the 8th (last preabdominal) somite; and is an older charac-

> ter than the loss of the first somite, since it is present already in the Protoscorpiones.

This view is given also elsewhere (Petrunkevitch, 1948).

Here is then quite a group of claims regarding the scorpion from this American school: (1) that the 7th and 8th tergites of modern scorpions represent a single segment, (2) that this is connected with the absence of an abdominal neuromere, (3) that the subdivision of a segment into two rings strengthened the tail, (4) that the early known fossil scorpions had an extra tergite. All these claims seem to be contrary to the views of other experts, and reasons can be given to doubt them all!

That there is a neuromere short is not surprizing. Were the scorpion less primitive we might expect more than one missing; for in its post-abdomen it has 5 segments which have lost all their appendages, and whose main function is to constitute a universal joint with which to apply the sting. Buxton's suggestion that a segment has subdivided "in order to give to the base of the tail greater strength" is indeed strange: there would seem more reason if it had segments united for that purpose, as in the last abdominal segments of Malacostraca. As to the early scorpions having a pregenital tergite, as must have been the case in their ancestors: this may be so; but the known Silurian scorpions are only three in number, and as neither Thorell & Lindström, nor Pocock who described the specimens of *Palaeophonus;* nor Whitfield, Thorell, Pocock, and Clarke & Ruedemann who discussed *Proscorpius osborni* suggested the extra segment, the writer feels that we must await better specimens and further opinion before we can accept the view that Silurian scorpions exhibit 13 terga between cephalon and sting. The writer believes accordingly that all scorpions from Silurian to Recent exhibit next to the cephalon the tergite of the second post-cephalic somite; and that they all exhibit 12 tergites between cephalon and sting. In Silurian time, however, the pregenital tergite may have existed, and if so, it was probably covered by the head and the tergite of the 2nd abdominal segment, as is described below for the eurypterids.

As regards the situation in the eurypterids, Clarke & Ruedemann (1912) homologized the 12 terga of the scorpions, Silurian to modern, with the 12 terga of the eurypterid, which therefore also would have 13 somites in front of the tail spine. Börner (1914, p. 681) and Versluys & Demoll (1923, p. 175) do the same. Størmer however (1934, p. 13) homologizes the 1st tergite of the eurypterid with the lost tergite of the pregenital somite of the scorpion and accepts the view that the 8th post-cephalic somite of the latter is represented by two tergites as claimed by Buxton and by Petrunkevitch. The latter (1948b) repeats his previously expressed views regarding the scorpion, and, regarding the eurypterid, agrees with Størmer, and says:

> If the first of the tergites were homologous with the first tergite of scorpions, as J. Versluys and R. Demoll accept, then one would be forced to assume the formation of a secondary segment as in scorpions, a possibility which one could not deny, but direct evidence for which is lacking.

On the contrary the first tergite in the eurypterid is that of the second post-cephalic somite; and the evidence for this was given by Holm's figures and description already in 1898 as explained below; but there is no need to invoke sub-segmentation to preserve the arachnid "12," which the above argument by Petrunkevitch acknowledges as unlikely. On the contrary, there is good reason to believe that the earliest history of scorpion and eurypterid were one and the same.

In the common ancestor of the xiphosure, the eurypterid and the scorpion (and so also of the other "Arachnida"), the appendages of the 1st abdominal segment advanced forward under the head between the coxae of the last pair (VI) of cephalic appendages to close the mouth space behind. These form the appendages called chilaria in *Limulus* and coalesced appendages, the metastoma, in eurypterids, which, indeed are like a pair of chilaria united together. In scorpions, however, with their change to a terrestrial life, the metastoma ceased to be useful in that way, was reduced, and forms the so-called "sternum," which again is a modified pair of appendages. This is not the view of arachnologists in general, and needs confirmation by careful study of the ontogeny; but it is the view of Vachon (Grassé, 1949, p. 390–1) and the writer.

Accompanying this forward migration of

the appendages of the pre-genital segment the tergum of the same was drawn down and under the head. In *Limulus* only the axial part has slipped under the head, the pleura still remain outside. But in the eurypterids where the pleura are reduced the first post-cephalic tergum was drawn down and under, and almost disappeared; whereas in the scorpion the somite is only traceable in the embryo except by its appendages, represented by the bifid sternum. In this, as in other respects, *Limulus* is the most primitive of modern chelicerates.

That the situation in the eurypterids was as here claimed is evident from study of the literature. Very fortunately the exoskeleton of a typical eurypterid is known in great detail, for in the Upper Silurian limestone of Rootziküll in the island of Oesel off the Gulf of Riga the exoskeleton of *Eurypterus fischeri*, both as complete individuals and as scattered parts, is exquisitely preserved, and has been studied in detail by a succession of workers, notably Niezkowski, Schmidt and G. Holm. The excellent preservation makes this species of enormously greater value than any other for morphological comparisons with other chelicerates. Already in 1883 Schmidt contrasted, by his figures and description, the gap between the cephalon and the 1st abdominal tergite (greatest in the middle and diminishing to each side) with the connections between the abdominal tergites themselves. Each of the other tergites has an anterior articulating projection extending under the posterior doublure of the tergite in front exactly as obtains in trilobites throughout the body from head to pygidium.

Holm, however, with his superior technique of isolating the fossils from the limestone matrix by acid, was enabled to give us a detailed account of the space behind the cephalon. He wrote (1898, p. 8,9):

> At the sides a doublure is lacking, and the head-shield is here connected by a suture with the first tergite as by a hinge. But within these arise sharply on both parts a doublure-like structure, which continues for a little stretch the hinge-like connection, but soon passes into a true doublure both on the hind border of the head-shield and on the front border of the tergite. The head-shield is here, as is always from the outside, separated by an open space from the first tergite. The doublure of the hind border of the head is even and directed completely to the front. That of the first tergite on the contrary is first directed to the rear, but soon bends to the front and passes here into a very thin torn joint-skin, from which also often rags extend into the front edge of the doublure of the hind border of the head. It is by this thin joint-skin that the connection between the head and the first tergite and therefore the bridging of the gap is brought about. In consequence of this joint-contrivance the mobility of the joint between head and thorax must have been very great.

Holm thus describes in detail and figures very well this junction (1898, pl. 4, fig. 15); but, knowing nothing of the pre-genital segment of the arachnid nor of the modern interpretation of the metastoma, in the writer's opinion he interprets it quite wrongly.

This connection is very different from those between the tergites themselves in that:

1. There is an uncovered gap at the surface.

2. The hind border of the head is more concave, and the doublure is wider than on the tergites behind.

3. The first tergite, instead of having an articulating extension passing forward under the head as in the trilobite, and as obtains between the postcephalic tergites themselves, has a considerable "doublure" passing *rearward*, fully half as wide as that of the head.

4. This "doublure" is reflexed forward again and extends as a thin membrane to the edge of the posterior doublure of the head, to which it is united.

These differences are highly significant; and, in the light of our knowledge of the pre-genital segment of the scorpion and of *Limulus*, their interpretation seems to the writer perfectly clear. Størmer and Petrunkevitch are in error: the twelve clear terga between the head and the tail spine in the eurypterid are the same twelve which we see in the modern scorpion.

Vachon, who suggests that the 1st abdominal tergite of the scorpion is a coalescence of those belonging to the original 1st and 2nd segments (Vachon, 1949, p. 390) is in error, also. The first tergite belongs to postcephalic segment 2. But the eurypterid exhibits an intermediate stage between the condition in the trilobite, where the tergite of the 1st post-cephalic segment is in place behind the head and the condition in the

scorpion, where this has entirely disappeared.

The splendid state of preservation of *Eurypterus fischeri* enabled Holm to leave us the evidence. His supposed joint-contrivance with wonderful mobility is no more and no less than the reduced pre-genital tergite withdrawn and almost buried beneath the head and the succeeding tergite, which last has moved up into the place which the pre-genital had previously occupied.

In this form, a typical eurypterid, the secondary function of the appendages of the pre-genital segment had caused them to advance far in front of their original position beneath the abdomen and this had caused the tergite of this segment to be drawn down and forward towards these appendages which had become the metastoma.

This explains why the rear of the cephalon is so concave and bears a very wide doublure: some of the posterior margin of the head has been drawn in and forward and added to the original doublure. This migration of the original 1st post-cephalic tergite was accompanied by the advance of the second with its appendages up to the head; and, since when these changes were initiated the 1st tergite was just as strong as the 2nd, we can see why the weaker articulating projection of this 2nd tergite was also drawn down and bent under to form a unique "doublure" under the front of this tergite. On this view the tergite of the pre-genital segment is still traceable in greatly reduced form in the Upper Silurian *Eurypterus fischeri*, being represented by the strip of membrane connecting the doublure of the head with the unique so-called "doublure" under the front of the following unreduced tergite.

There can therefore be no doubt but that the eurypterids and scorpions have the same tagmata and the same segmentation, which are the result of a common early ancestry. Were the views of Petrunkevitch and Størmer correct, though each group has 12 evident segments between head and tail spine, only the last four of these would be homologous with one another! Also, on the claims made above, the 1st abdominal tergite of the scorpion is that of the 2nd somite and not the coalesced 1st and 2nd as Vachon claims (1949, p. 390, 391).

The 15th post-cephalic segment and the absence of a telson in eurypterids and scorpions.—It has been claimed above that these two groups have the same tagmata and the same segmentation; that the 1st evident tergite of the 12 between the head and the tail spine belongs to the 2nd post-cephalic somite; that the tail spine of the first and the sting of the second are homologous with one another; and that they are not telsons (or analites), but represent normal segments very far in front of the primitive analite of their ancestor. Reason has also been given for the view that the 12 evident post-cephalic tergites of the scorpions and eurypterids are homologous with one another.

The question now arises: to what segment do the tail spines belong? On the basis just given the tail spine or sting would represent the 14th segment, not the 15th as in *Olenellus*, which has been so fruitful in suggestions. Therefore we are justified in looking round to see if any consideration has been overlooked. This suggests the history of development of our knowledge of the Crustacea. Within this subphylum the "lower" classes are varied, mostly reduced and degenerate, but the Malacostraca embrace both primitive and specialised forms, both of which allow of close comparisons with the other arthropod classes. Till comparatively recently the body in general was divided into head, thorax of 8 segments and abdomen of 6 together with a telson; and the telson was on this scheme behind 14 post-cephalic segments (Calman 1910). But within the Malacostraca are included the Leptostraca represented by *Nebalia* and a few other forms. These differ from the higher, the Eumalacostraca in three ways, of high significance for our present problem: (1) the Leptostraca (e.g., *Nebalia*) have an extra segment in the abdomen; (2) the last or 7th "abdominal" segment bears no appendages; (3) the "telson" bears a pair of appendages (caudal rami or caudal furca). In *Nebalia* the last normal segment is thus the 15th as in *Olenellus*. Then, within the Eumalacostraca in *Gnathophausia*, one of the Mysidacea, a very primitive order, the last abdominal "segment" is clearly a coalescence of two. In many other Mysidacea it is twice as long as the neighboring ones in front (see Tattersall, 1951). An example from another order is *Anaspides*

—in this division, the Syncarida, indeed the coalescence of the last two normal segments can be traced in the paleontological record.

The facts strongly suggest that where the appendages of the 15th post-cephalic segment had important functions for locomotion, their muscles extended through the segment in front, and these two segments became coalesced into one. In the Leptostraca, however, where the caudal furca was retained, the appendages of the last segment were lost and this segment in consequence did not coalesce with that in front. The Malacostraca thus agree with *Olenellus* in having 15 somites behind the head.

Returning now to the chelicerates: the eurypterids and scorpions inherited a greatly developed axial spine primitively of importance for locomotion, and perhaps for righting the body after swimming upside down; but owing to their ancestor's mode of life they had entirely lost the appendages from the posterior segments that they retained. As a result of the great use of this spine, which monopolized its segment as in *Olenellus*, the muscles which moved it (i.e., the intersegmental muscles between it and the segment in front) may, from analogy with the case of the uropods in the Malacostraca, be expected to have spread through a further segment and caused the coalescence of the two.

On this view the 12th or last apparent abdominal segment of these forms is a double segment; and as the first of the twelve is the tergite of the 2nd postcephalic somite, it represents the 13th and 14th post-cephalic, making the tail spine of the eurypterid and the sting of the scorpion the 15th post-cephalic, as in *Olenellus*. In very many scorpions the segment ring in front of the sting is much longer than those in front and hence supports this view.

In the Crustacea we still have an extensive hind gut and we have what is called a telson, in front of which the formation of segments takes place. Comparisons with polychaets and trilobites suggest that this represents the telson of the annelid together with the undeveloped segments between this and the 15th post-cephalic.

In the chelicerate we have so short a hind gut that it is practically non-existent; and the writer suggests that here the telson is quite absent, that the anus is secondary, and that in the forms now being considered the body ends with the 15th post-cephalic segment.

In the Olenellidae, as we have seen, quite a variety of modes of termination of the body are exhibited; and they suggest that after the opening of a new anus under the last important organ (either an axial spine or a pair of pleura), the segments behind were reduced or aborted.

This must be the case in these eurypterids and scorpions with 15 post-cephalic segments ending in the great tail spine. Behind this there is here no evidence of reduced segments, so nothing can be said as to their mode of abortion. The tail spine has nothing in common with a telson: even the anus under it is no part of a telson but is secondary. This absence of a telson constitutes one of the most important distinguishing features of the chelicerates.

Few morphological features have been more consistently misinterpreted than the various terminal members of the body in chelicerates. Here we have tail spines which are called "telsons" and are identified by zoologists with the post-segmental anus-bearing telson of the polychaet. Sometimes they are referred to as a terminal appendage or an appendage of the previous segment. But by all they are called telsons. This arises from the position of the anus. But as explained early in this paper the olenellid trilobites prove conclusively that this view of their morphological significance is wrong and gives very strong reason to believe that the anus in all chelicerates is secondary. This is strongly supported by the shortness of the hind gut.

The appendage-bearing post-cephalic or abdominal segments of eurypterids.—Since the eurypterids and the scorpions, as well as *Limulus*, have each morphologically behind the cephalon a pre-genital and a genital segment and the equivalent of five pairs of gills behind the genital apertures, it would appear extremely probable that the appendage-bearing segments and gills in the three groups are homologous.

Current opinion, however, not only gives them different tergites, as discussed and opposed above, it also gives them different appendage-bearing segments, namely, post-

cephalic 1–6 for the eurypterid against 1–7 for the others.

As regards the first somite and its appendages, there is perhaps no longer any doubt. *Limulus* presents us with the appendages of the pre-genital segment in their most primitive form, the chilaria. With this are equated the bifid metastoma of the eurypterid and the sternum of the scorpion (Millot & Vachon, 1949, p. 391, and the present paper).

It is very unfortunate that we have so little direct evidence of the character and attachment of the gills in eurypterids. The point in doubt has been whether the genital segment bears gills or not; but the question also implies others, namely, to which somite each pair of gills belongs, and how they were attached.

Laurie (1893) was the first to note evidence of the number of gills, five pairs in a specimen of *Slimonia acuminata* Salter; but, regarding the first ventral plate as the genital operculum and believing in a relationship with *Limulus*, in which this plate bears no gills, he suggested that the first gill was not attached to the so-called "operculum," behind which it lay, but that it belonged to the next segment, and was attached to the ventral body wall; whereas the others, he thought, would be attached to the dorsal surface of the plates. In this way the five pairs of gills were attributed to the abdominal somites 3–7. This has been supported by Moore (1941), except that he claims similar attachment to the ventral body wall for all the gills.

If the chelicerates are descended from trilobites, the prototype of their limbs, cephalic and post-cephalic, was the biramous limb of the latter, which, as Størmer has claimed, is represented in highly modified form by the gill-bearing appendages of *Limulus:* also for very much longer it had been accepted that the endopodite and exopodite of the crustacean were represented in it. But to recognize such a limb in the eurypterid and the scorpion (except for the trilobite-like "exopodite" in the pecten of the latter) is difficult, because all known examples of these are so vastly more specialized than is the modern *Limulus*, notwithstanding that eurypterids and scorpions occur as early as the Ordovician and Silurian respectively. In the eurypterid, too, we have only extinct forms, of which only the exoskeleton is known, and that very incompletely.

There is no need to attempt to prove that the lung-books in arachnids represent the gill-books in *Limulus*, and that in the eurypterids also the homologue of the same must have existed; and the question of their distribution can straightway be considered.

That there are only five pairs of movable ventral plates and five pairs of gills in eurypterids, and that the first gills lie dorsad of the posterior part of the so-called "operculum," is suggested by several fossils: *Slimonia acuminata* Salter, *Eurypterus fischeri* Eichwald, *Eurypterus* (*Onychopterus*) *kokomoensis* Miller & Gurley, *Carcinosoma scorpionis* (Grote & Pitt), *C. newlini* (Claypole), *Mixopteris kiaeri* Størmer, as indicated by Laurie, Holm, Clarke & Ruedemann and Størmer. Furthermore, both the ventral plates and the gills occur regularly at segmental intervals, which has suggested that the gills belonged to abdominal somites 2–6. On account of this discrepancy between *Limulus* and eurypterids Moore (1941) restudied the specimen of *Slimonia* on which Laurie had based his restoration of this part, and he thought that he had surmounted the difficulty and could homologize the abdominal appendages of the eurypterid with those of *Limulus* and the scorpion by certain assumptions; namely, that the gills covered by the operculum and by each of the following four plates were all free from the dorsal surfaces of the plates and were highly vascular areas of the ventral body wall; that the first gills belonged to the first post-genital somite; and that this somite bore no ventral plates.

Such a theory will surely satisfy no one, for the ventral plates including the so-called "operculum," though overlapping, succeed one another with segmental regularity, and at segmental intervals, just like the terga of the same segments. The plate following the "operculum" is not segmentally the next but one, but the very next, and whatever applies to the first post-genital somite applies also to the next three behind. A simple diagram will easily show that the theory is false, for if there were no ventral plate for the first post-genital segment, the next

plate would not be overlapped by the so-called "operculum." In the writer's view no one has hitherto interpreted correctly these abdominal organs in the eurypterid; and we must look for a more acceptable theory. Also considering: (1) the close correspondence between the book-gills of *Limulus* and the lung-books of the scorpion, (2) the strong suggestions of close relationship between the eurypterids and the scorpion and (3) the evidence advanced in this paper of the derivation of all chelicerates from the trilobites, it seems to the writer extremely improbable that the gills of the eurypterid were merely vascular areas of the ventral body wall.

Regarding these ventral plates, the writer begs to offer a quite new theory of their morphology. Here, as in many other cases, we must avoid being misled by an antiquated terminology. Behind the cephalon and opposite the first six tergites of the abdomen corresponding to its abdominal somites II–VII, in all eurypterids the ventrum is bounded by five plates which are apparently pairs coalesced in the mid-line. Each has the length of two tergites. They overlap one another rearward like tiles on a roof, but inverted, the first overlapping the anterior half of the second and so on; from which it follows that the five plates cover the length of six segments. Also, in the numerous cases where gills are indicated, these are covered by the posterior halves of the plates. The first plate is called the "operculum" from a function of the first pair of abdominal appendages in *Limulus*. The other four are usually called sternites; but since the time of Niezkowski (1859) and especially of Schmidt (1883), who was the first to give an account of the whole body from well preserved specimens, it has been believed that all were pairs of appendages; and Holm (1898) called them leaf-feet (see Text-fig. 8A–D).

Laurie's restoration of *Slimonia acuminata* (1893, pl. 2, fig. 9), often reproduced, is an exception to the system just described in exhibiting pairs of plates showing sternites partly covered by them; but it has been criticized by Størmer (1934) and by Moore (1941), and there is no sufficient reason now to suppose that *Slimonia* is any exception to the rule.

In Schmidt's longitudinal section (1883, pl. 3a, fig. 1c) which Holm did not replace, each plate is represented by two close lines indicating the theory of a thin appendage (leaf-foot) believed to be attached to a membranous ventral body-wall at the anterior end. Lying horizontally as they do, we can distinguish these two supposed faces as dorsal and ventral. Holm accepted Schmidt's interpretation and, through isolating the sclerites, added the important fact that each ventral sclerite except the so-called "operculum" had a very narrow doublure at the anterior end as well as a wider one at the posterior; and that both were on the dorsal side! This reminds one of the state of things on the first tergite described above, and if we had to explain it, we might attribute it to a slight forward shift of all the sclerites.

Each ventral plate, however, is compound, not only across the median line, being a pair but also by a transverse division; for though the "operculum" is divisible into three successive strips (Text-fig. 8D), each of the other four is divided into two, an anterior and a posterior strip, each of them closely comparable in size with a tergite. It has been assumed that this line of subdivision is an inheritance from a jointed arthropodan appendage, but the transverse line of division is a close row of "scale markings" (Clarke & Ruedemann, 1912, p. 25), and indicates a special attachment and boundary of muscles along it. In front of it the scale markings, which almost cover the surface are somewhat smaller than are those behind (Holm 1898, pl. 5, fig. 10,11; pl. 6, fig. 1,2,5, 6; pl. 7, fig. 2,3,5–8, all photos). It was assumed by Schmidt that each plate was a pair of appendages attached at its anterior edge. Holm accepted this conclusion, which, so far as the writer is aware, has not been opposed. The writer's view, on the contrary, is that each is a compound of a sternum in front of the transverse line and an appendage pair behind it. Taking as an example the last plate, the exposed part of which is opposite the sixth tergite (that of the seventh abdominal somite), this exposed part alone, with the gills which it covers, is the simplified and specialized pair of appendages (exopodites) of the 7th abdominal somite, and is free in the water: its dorsal (or posterior) surface is attached at the anterior limit of its segment to a membranous sternum of the

same (S XIII of Text-fig. 8C), and protects its pair of gills, presumably lamellar. Dorsad is the 7th abdominal sternum. Unlike all the sterna in front, it is membranous, in accord with the fact that the appendages of the 8th somite are quite lost. The anterior half of the plate almost covered in ventral view, hidden by that in front, is the sclerotized sternum of the segment in front, the 6th abdominal somite (S XII). This moved, however, with the plate-appendages ankylosed to it, and limited their movement. The writer applies a similar interpretation to the next three plates in front, except only that the sternum covered by the posterior gill-bearing half of each is sclerotised for the above mentioned function.

Coming now to the so-called "operculum," this differs in three respects from the four plates, each leaf-foot plus sternum, behind it (Text-fig. 8D).

1. Instead of only two sub-equal transverse strips, we have in front of these in the best preserved specimens from Rootziküll a third narrower strip both in *Eurypterus fischeri* and in *Dolichopterus laticeps* (Holm, 1898, pl. 4, fig. 18,23; pl. 5, fig. 10; pl. 6, fig. 1,2), which in life was largely hidden behind the metastoma and the coxae of the great legs. In *Eurypterus* the division lines in each case are a row of scale markings, but Størmer regards each of them as joints in a gill-bearing appendage (1934, p. 44).

2. Instead of the right and left halves coalescing in the mid-line, these are here separated.

3. This separation is effected by the presence of the median genital appendage, which is of two types indicating the sexes.

Thus two new parts here appear, the median genital appendage and a narrow more anterior transverse strip: it is still more compound.

The larger median genital appendage, interpreted by Holm as the female, but by Gaskell and by Størmer as the male, in several forms suggests very strongly a pair of endopodites (telopodites). It commences in front with a pair of triangular lobes behind the narrow anterior strip of the "operculum," best seen in *Dolichopterus laticeps* (Holm, pl. 4, fig. 23), following which the median appendage is still a pair united along the median line. In the species named it extends across four somites, in *Eurypterus fischeri* over three and a half. Laurie had suggested for *Slimonia* that the triangular lobes mentioned above formed the sternum of the genital segment. In *Eurypterus* in the same sex the plate next behind has also a median appendage accessory to the larger one on the genital segment; but there is not here, nor in any other plate behind, any trace of the third transverse front strip.

If the so-called "operculum" as a whole is closely compared with the four ventral plates behind, it will be seen that one cannot but serially homologise its two posterior transverse strips with the two strips of the latter (Holm, 1898; compare pl. 4, fig. 18,23; pl. 5, fig. 10; pl. 6, fig. 1,2,3 with pl. 4, fig. 21; pl. 6, fig. 5,6; pl. 7, fig. 5–8). Hence, in the writer's view, the posterior strip of the "operculum" with the gills covered by it represents the exopodite of the following or 1st post-genital segment. The middle strip is the sternum of the genital segment, the appendages of which are represented only by the median genital appendage, a coalesced pair of endopodites, which are coalesced also with the sternal plates. The anterior narrower strip is unique; and from its position, size and character, is best interpreted as the sternum of the reduced pregenital segment, the appendages of which, the metastoma (coalesced coxae) stand immediately in front.

On this view the genital segment bears no gills or their equivalent, as also is the case in the scorpion and limulus. The so-called "genital operculum" is highly compound: it is not even mainly the appendages of the genital segment. Only the median genital appendage represents these, and this, in the presumed female in *Eurypterus*, is very small indeed. Most of this plate is divided between the sternum of the genital segment and the exopodite of the 1st post-genital; and these, together with the anterior strip, form no part of the appendages of the genital segment.

Thus the "operculum" is mainly the genital and pregenital ventral body surface; but quite continuous with this are the exopodites of the 1st post-genital, bearing their gills in a free water space of only half the

area assumed by Schmidt. It should be noted that on the genital segment the ventral surface is sclerotised, only where there is no appendage retained. After all these parts coalesced, the muscles moved the plate as a whole except for bending, both in respiration and in swimming, probably upside down as Patten (1912, p. 371) and Størmer (1934, p. 62) claimed.

Leaving the unique anterior or genital plate, let us turn again to the remaining four. Unlike the theories of Laurie and of Moore, which have above been discarded, those of Schmidt and Holm and of the writer apply to all the abdominal somites which bear appendages, and will here be contrasted in detail.

Theory of Schmidt and Holm in modern form: Each ventral plate belongs to a single segment, the four posterior belonging to the first four post-genital segments. Each is a specialised coalesced pair of exopodites, with dorsal and ventral walls of the same area twice as long as a segment, the distal and exposed half bearing and covering a pair of gills; the whole being attached at the anterior end to a membranous ventral-body wall.

Throughout the whole length, where these plates overlap one another, a penetration across the plates (not counting gills encountered) would traverse external cuticle *five times.*

On this theory the so-called "operculum" is the more complex appendage of a single segment, the genital, and bears gills; and the appendage-bearing segments are five altogether.

Theory of Raw: Each ventral plate is compound, the anterior, normally covered half being the sclerotised sternum of a segment, to the rear of which there is ankylosed a pair of exopodites covering their gills and belonging to the segment next behind. The anterior half of each plate is thus the ventral body wall. The dorsal wall of each ventral plate is limited to the posterior half and is the posterior wall of appendages.

Where the plates overlap a penetration across the plates, not counting any gills encountered, would traverse external cuticle *three times.*

On this theory the so-called "operculum" embraces parts of three segments, and because it comprises endopodites of the genital and exopodites of the first post-genital, the five plates represent and also bear appendages of six segments, the genital and five post-genital, as in the scorpion and limulus. As, however, it also includes the sternum of the pre-genital, the five plates represent seven segments—abdominal somites 1–7.

The contrast between the three theories above discussed is expressed in the longitudinal sections.

There is reason to believe that the motions of these plates were limited. If the theory of Schmidt and Holm were correct (i.e., that they were each nothing but appendages, attached only at the anterior end to the membranous ventral body wall) then we might expect, in dismembered fossils, to find the plates frequently turned the wrong way. But it is noteworthy that they are always turned to the rear. This is completely explicable on the writer's theory and would result from the dorsal surface of each plate, at its anterior limit opposite the mid-length of its ventral surface and just behind a line of muscles, being attached to the anterior edge of the next plate behind. Those muscles would act in expelling the water around the gills in respiration and also in swimming. Only limited motions would be needed for these functions.

It may be asked how the sternum of a segment became coalesced with the following appendage, and how it also came to be marked along the axial line; but in the trilobite ancestor both sternum and appendage were so little sclerotised that usually neither is preserved at all. The sclerite of both developed together, and in harmony, in response to what was useful for the mode of life.

This interpretation of the abdominal appendages of eurypterids is strongly supported by what is known of scorpions. Here we have living animals whose complete anatomy and ontogeny are available for study.

Much has been written on the habitat and mode of life of the Eurypterida. Størmer reviewed it and discussed it at length in 1934. The last pair of legs except in *Stylo-*

nurus are paddle-like and have been supposed to function in swimming but he states (1934, p. 62)

> the swimming function of the Eurypterida was not only due to the last pair of prosomal appendages but also to a large extent to the plate-shaped mesosomal appendages.

Patten, already in 1912, had expressed the view that they would swim on their backs like the young *Limulus*. However, they would rest on the bottom right way up; and the principal function of the last pair of legs would be, the writer thinks, to clear a space beneath the abdomen sufficient for the respiratory movements of the abdominal appendages with their gills.

The appendage-bearing abdominal segments of scorpions.—Instead of 12 segments plus telson as of old, or 13 segments plus telson as has been accepted since Brauer's discovery of the pre-genital segment, these segments are claimed above to be 15 but no telson and a secondary anus in place of the latter.

Seg. VII, the pre-genital. Owen in 1872 claimed that the chilaria of *Limulus* were a pair of appendages, and Lankester claimed that these were homologous with the "pentagonal and sternal plate of the scorpion." This is accepted by Vachon (1949) and the writer. The true sternum of this segment can perhaps no longer be recognised.

Seg. VIII. The external genital organs can be claimed, at least on the basis of *Limulus*, as involving a pair of modified appendages.

Seg. IX. The combs or pectines are easily recognised as its appendages limited to the exopodite. They constitute the most primitive abdominal appendages visible in the chelicerates, for they present much the closest approach to the gill branch of the trilobite. This could be attributed to their restricted use, namely in copulation. Besides their unique form, they occupy a unique position, for they lie on the first macrosomite of the abdomen (the 3rd segment), which was macropleural in the olenellid ancestor.

Segs. X–XIII. It is now perhaps universally recognised that the four pairs of lung books must represent respiratory appendages of an aquatic ancestor. Like the pectines they must represent the gill branch or exopodite of trilobite appendages, and their form is attributable to the change to aerial respiration In their aquatic ancestor, as in the eurypterids, the lamellar appendages extending across the venter gave water free access to the gills behind them, but on the change to terrestrial lungs the access of air was restricted to a pair of stigmata.

In Paleozoic scorpions the stigmata cannot in general be seen (Petrunkevitch, 1949, p. 134) but Peach (1891, p. 399,400) records slit-like spiracles at the postero-lateral angles of the plates in *Eoscorpius tuberculatus* and *E. glaber*. In Triassic time, too, as recorded by Wills, the stigmata were still mostly sub-marginal through the doublures of the plates in beautifully preserved material. Hence it would appear that it is mainly since Trias time that the stigmata have migrated on to and over the ventral surface and reached their present sites.

The ventral surfaces of these book-lung segments are called sternites, but comparisons with eurypterids strongly sugggest that each is derived from a united sternum and pair of appendages. Further, the part externally visible in the eurypterid and opposite to the corresponding tergite is, on our theory, the pair of appendages. In the scorpion too they do not appreciably overlap and are essentially modified appendages (compare Text-fig. 8E with 8C). At the change from water to air the loss of swimming function might well lead to reduction of the sternum rather than of the appendage. That these sternites are pairs of appendages rather than sterna is supported by their bilobed form in the Carboniferous *Eobuthus* (Wills, 1925, pl. 3, fig. 2,12,13; also, Fritsch, 1904, and Pocock, 1910) and the Triassic *Mesophonus* (Wills, 1947, text-fig. 13,14), and also by the position of the lungs in the four lung-bearing segments. At the change from water to air the proportion of free oxygen in the medium around them would increase so greatly that this would need replacement much less frequently. Owing to the recent work on fossil scorpions it is now easy to envisage the transition from respiration by book gills to that by book lungs.

Relationships of the Eurypterida and Scorpionida: their phylogeny and classi-

fication.—These two orders have submitted above to extremely close correlation: they have the same segmentation, their bodies have the same tagmata and comparable appendages. Both are claimed also to agree in segmentation with the Lower Cambrian trilobite *Olenellus* which is claimed to be derived from their pre-Cambrian common ancestor. Indeed so close is the comparison that each helps to interpret the other.

1. Both have at least 13 somites, and probably 14 between the prosoma and the tail spine.

2. In both, the appendages of the 1st abdominal segment advanced under the cephalon and became coalesced as the "metastoma" and the so-called "sternum" respectively. Behind this in both is a genital and 5 appendage-bearing segments.

3. In both the tail spine is not a telson, but represents a normal segment.

4. In both the anus is claimed as a secondary opening.

There are few distinctions of importance between them. The eurypterid is aquatic and has compound eyes. Those would be lost by the scorpion when it became terrestrial. The first post-genital pair of appendages of the scorpion also are unique in character; but in their form they are primitive and have their prototype in the gill branch of the trilobite. Both orders, therefore, have primitive features and as both can be derived from the same chelicerate and trilobite ancestor, they should certainly be included in the same class. The nature of their differences, however, indicates how early was their divergence. The Ordovician eurypterids do not differ appreciably from later forms; but the scorpion's pectines differ so enormously from eurypterid appendages and are so much nearer to those of the trilobite ancestor that it is very probable that already in pre-Cambrian time the Scorpionida and Eurypterida had diverged.

In contrast, according to arachnologists, scorpions belong to the same class Arachnida of the subphylum chelicerata as even the mites and ticks or Acari with few abdominal segments, whereas the Eurypterida are put in a separate class, the Merostomata, in association with the xiphosures, which also have a different segmentation. This is the classification of Vandel (1949) and, as regards Arachnida, of Petrunkevitch (1948, 1949). Also the trilobites, from which they are here derived, though from pre-Cambrian forms, are, by Vandel, not even included in the Eu-arthropods, but are given the rank of Pro-arthropods, i.e. forerunners of the arthropods; and Petrunkevitch, too, does not derive any chelicerate from them. Further, the latter has recently reclassified the Arachnida and the two orders of Scorpiones and Acari are placed in the same subclass, the Latigastra; whereas the Eurypterida as well as the Xiphosura form two separate classes of chelicerates (1948)!

Petrunkevitch's views are very different from those of the writer. According to him the chilaria of *Limulus* which he acknowledges as appendages have no counterpart elsewhere: in the eurypterid the metastoma is a sternite, not a coalesced pair of appendages, and so also is the "sternum" between the posterior coxae of the prosoma of the scorpion.

It should be noted also that Petrunkevitch agrees with Størmer in attributing to the Eurypterida and the Scorpionida the same number of primitive abdominal somites, but different tergites except for the last four, and different respiratory somites. According to Petrunkevitch "the different classes followed their own courses of evolution." In his 1949 paper (p. 293) he discusses the evolution of the Arachnida, but he has no use for the trilobite in the phylogeny, and he claims that a first step in the evolution was the restriction of the abdomen to 12 segments, the sting being merely "a dorsal post-anal outgrowth of the body wall," views which have above been opposed.

6. CHELICERATES WITH 12 SIGNIFICANT ABDOMINAL SEGMENTS
(Text-fig. 9A,9B)

As 12 is the number of abdominal segments which have been regarded as primitive in the "Arachnida" by Petrunkevitch, it is not surprising that no less than 5 orders of Arachnida as well as 3 orders of merostomes have their abdominal segmentation based on 12. They are: *merostomes*—Aglaspida Raasch, Beckwithida, n. order, and Synxiphosura; and "Arachnida"—Pseudo-

scorpiones, Haptopoda, Phrynychida, Araneae and Solifugae.

The aquatic orders are here shortly reviewed:

Aglaspida

For our knowledge of the group we are indebted to Raasch (1939), who has not only for the first time adequately described the known forms, but has also himself collected the great bulk of the material. He includes in the order *Beckwithia typa* Resser and *B. major* (Graham), which here are excluded as belonging to a distinct order. Of the 19 species remaining, spread through nine genera, all but four were discovered and first described by him.

This order is of special interest because it includes the earliest of known chelicerates, coming as they all do from the Upper Cambrian; and, as might be expected, they are the most primitive. Their rarity is explained below.

After giving a systematic description of all species in his Part I, Raasch discusses the morphology in Part II, the homology and phylogeny in Part III and the distribution in Part IV.

Characteristics and segmentation.—The Aglaspida (leaving out *Beckwithia*) are a very compact order, the genera differing only slightly from one another. All are very similar to *Olenellus*. They, too, have an ovoid outline except for a great tail spine, a semicircular head shield with large posterolateral or genal spines, a pair of compound eyes and absence of facial sutures; but an abdomen of 11 free segments diminishing in width to the rear, and all with large falcate pleura; followed by the tail spine. Also, as in all primitive trilobites, the dorsal integument throughout is very thin and that of the ventral surface and appendages is still more delicate, so that about these very little indeed is known. But what is known, from a unique specimen of *Aglaspis spinifer* Raasch, suggests that, unlike *Olenellus*, there were no antennae, for such have never been found, whereas this species is claimed to exhibit a pair of chelicerae with four joints, under the front of the shield, and traces of leg-like appendages, both cephalic (5 pairs) and abdominal, behind these as far as the 8th abdominal (p. 12,13). Most olenellids have an areolar pattern on the dorsal integument but some, such as "*Olenellus*" *argentus* Walcott (?Esmeraldina) (Walcott, 1910, pl. 40, fig. 16) and *Kjerulfia? granulata* Raw (Raw, 1936, pl. 20, fig. 4a–5) are granulated, and in the last named the granules are centrally pitted. In the Aglaspida the dorsal test is, in most, granulated, but in several it is pitted (Raasch, p. 51–56). The main function of the pattern is supposed to be to strengthen the shield, but it seems more probable that it was related to a sensory function.

The most conspicuous differences from *Olenellus* are the following: (1) the lack of dorsal furrows and hence weakness of the trilobation throughout the body, though this is not so weak as in the Eurypterida; (2) the lack of evident segmentation on the axial lobe of the cephalon; (3) the fact that the anterior articulating extensions of the terga extend out to the beginning of the pleural spine instead of being limited to narrow axial lobe; (4) the eyes, more compact, more approximated and more variable in position; (5) the tail spine being the 12th instead of the 15th abdominal segment; (6) that this spine-bearing segment is more developed and more specialized; (7) the presence beneath the base of this 12th abdominal segment of the "post-ventral plate"; (8) having a transverse pair of tubercles "post-axial nodes," down the mid-line at the rear of the cephalon, and also of the eleven segments that follow; (9) not having a conspicuous hypostome or labrum beneath the cephalon; and (10) not having antennae.

The eyes though compact, being a quarter to an eighth the length of the cephalon, are still of the trilobite type, the visual surface as indicated by the area of smooth instead of pustulose integument occupying the outside lateral halves of the circular walls of the optic tubercles. On this Raasch (1939, p. 60,61) remarks

> The apparent lack of ocular facets on dorsal and ventral surfaces [of the visual area] and the thick translucent ocular integument renders it probable that the eyes were sensitive to the quantity and direction of light, but were not image recording. The eye then is more primitive than that of most trilobites, of eurypterids and even of *Limulus*.

This one cannot accept, because the eye is a development of the compound *Olenellus*

type of eye, already very ancient in the Lower Cambrian.

Raasch remarks the absence of ocelli; but in *Chraspedops modesta* Raasch the cephalon exhibits behind the anterior margin of the head shield a pair of pits very much closer approximated than are the compound eyes. These may well be a pair of ocelli. Both their character and position favor this interpretation (see Raasch, 39,61; pl. 16,17).

With no sufficient reason Raasch divides the abdomen into pre- and post-abdomen; and in different cases he makes the 11th and 12th, or the 10th, 11th and 12th (with the spine of the 12th in each case) comprise the post-abdomen; and he states that the "post-ventral plate" underlies these two or three segments. This is discussed below. His pre- and post-abdomen bear no relationship with these so-named divisions in scorpions and eurypterids.

The tail spine he calls a telson-spine, and its segment a telson segment. As in the cases already discussed this is an error, if by telson is meant the primitive analite.

Under the broad anterior part of the tail spine segment is the unique "post-ventral plate," which he does not interpret, but states that it is conveniently regarded as a "sternite." It is seen in his pl. 1, a "ventral impression of the dorsal shield" of *Aglaspis spinifer*, where beneath the base of the tail spine is the mould of the ventral surface of the two halves of the "plate," with a narrow gap between them. On either side of the abdomen can be counted the 11 pleura of the other abdominal segments. Raasch says that it underlies the post-abdomen, which in this case he defines as comprising the 11th and 12th segments. From the pleura of the 11th segment one would judge that this segment is in front of the "post-ventral plate." This feature is, however, superlatively seen in his pl. 13, fig. 3, "Ventral aspect, ×6, of postabdomen covered by postventral plate in natural position" of *U-arthrus instabilis* Raasch (see Text-fig. 9B). He interprets this as segments 10, 11 and 12 in ventral aspect, for he says (p. 33) that the post-ventral plate underlies the 10th, 11th and 12th segments. But this is a unit isolated by dismemberment of the exoskeleton. Segments 10 and 11 are normal segments with projecting pleura. There is no reason to suppose that in dismembered specimens the tail spine segment would remain attached to the segments in front. This figure, pl. 13, fig. 3, is simply the ventral aspect of the tail spine. The "post-ventral plate" is a couple of quadrangular but almost semicircular plates approximated to one another along their long straight boundaries, 3.6 mm. long. Their homology he does not discuss, but the Olenellidae tell us what they are. In *Wanneria walcottana* (Wanner) the two pleura of the 18th abdominal segment are directed rearward and their posterior edges meet one another in the mid line, above whatever there was behind (Walcott, 1910, pl. 30, fig. 8,10–12; Resser & Howell, 1938, pl. 11). This is also the case in *Wanneria? pennapyga* Raw (Raw, 1936, pl. 21, fig. 3a,3b). In the latter case a pitted surface is dorsal. In *Aglaspis spinifer*, too, "the dorsal surface has a pustular structure" (p. 10), and "the post-ventral plate is pustulated like the dorsal shield, but with the pustules on the ventral surface" (p. 12). This indicates that the post-ventral plate is inverted. These plates are the enlarged pleura of the greatly developed 12th segment turned under the tail spine for its further support. The inversion, together with their posterior direction, causes their *anterior* edges to meet one another in the mid-ventral line. We must bear in mind that all pleura are appendages (Raw, 1953, p. 84–86) and were still moved by muscles in Aglaspida. The conclusion is inevitable: the "post-ventral plate," so-called, is simply the two pleura of the tail spine segment turned under it.

But if we look closely at Raasch's pl. 13, fig. 9 (Text-fig. 9B) a further tale unfolds. Behind the robust post-ventral plates and from beneath them another narrower pair of plates projects rearward again, meeting one another in the mid-ventral line. Another similar pair likewise projects beyond these, and still another pair beyond again! All these three narrow pairs of plates underlie the tail spine. Two or three of these narrow pairs of plates are seen also in a ventral aspect of the tail spine of *Chraspedops modesta* Raasch (his pl. 17, fig. 1). Thus, on this interpretation, not only the post-ventral plates, but the pleura also of three further segments are supporting the tail spine. But, considering how very much more robust are the post-ventral plates than the three fol-

lowing pairs of pleura, the tail spine was probably the last significant segment; and it is probable too that the acting anus had been *secondarily* opened beneath that segment, and that the ventral plates opened at defecation. Clearly the tail spine here is not a "telson" and does not represent a "telson segment" or analite.

Seeing that the abdominal segmentation is so primitive, the segments being so similar to one another and so similar, too, to those of the primitive olenellids, we cannot suppose that a segment in front has slipped out of sight as in scorpions nor that any of the "post-ventral plates" represent the pleura of more than one segment. We therefore reach the conclusion that the abdominal segmentation is 12 significant segments plus 3 reduced. Both of these figures illustrate the control by triads behind the head. The number of reduced segments is the same as in *Olenellus thompsoni* and in *Paedumias transitans* (Walcott, 1910, Resser & Howell 1938).

Raasch expresses very different ideas: homologizing the segments of the Aglaspida with those of eurypterids, it was apparently necessary for him to import another segment, and so he suggests (p. 71) that the tail spine is a union of the 12th segment with the telson-spine. *Olenellus* however, as stressed above, indicates that the latter is not a telson, but the development of the dorsal axial spine of a normal segment. Also, being a purely tergal structure, it has strong cuticle all round it. Re the post-ventral plate, though Raasch refers to it (p. 70) as "sternitic"; and (p. 65) states that "it is conveniently regarded as a sternite," on the contrary its strong cuticle indicates its derivation from the dorsal surface of the ancestral trilobite. That this is so is indicated by the fact that normally all the ventral surface fails to be preserved. As to its functions, he mentions (p. 65) "a protective exoskeleton," "the attachment site for strong muscles controlling the motion of the telson segment," and that the median cleft acted as a hinge by which the plate might assume a flat or a ventrally convex attitude. And he states that as the gills "could scarsely have been located on any of the first six abdominal segments as in Eurypterida, they were probably present beneath the post-ventral plate," and also (p. 71) that the gills "moved progressively forward in the development of the Merostomata from the aglaspid to the eurypterid stage." But gills are necessarily very delicate structures: the exopodites would be the more delicate part of the trilobite limbs and hence there is no reason to suppose their absence from the anterior abdominal appendages; and, as mentioned above under Eurypterida, the exopodites of the ancestral trilobite would best be retained in the anterior part of the abdomen in the clearest water, as is the case in eurypterids. What little is known of these appendages fully supports the conclusion based on their geological horizon, that they would be the most primitive among known chelicerates. Størmer, too (1944, p. 75, fig. 16b), gives a restoration of the ventral surface of "*Aglaspis eatoni*"; but his interpretation of the post-ventral plates is different from that of Raasch as well as from the one given above. They are regarded as modified sternites, but are represented not at all under the tail spine, but under the 10th and partly under the 9th and 11th abdominal segments. He represents, also, uniramous walking appendages throughout the body.

The disposal of the terga and pleura in the aglaspid is remarkable and unique. Besides greatly developing the 12th segment with its axial spine, the aglaspid retained the three following reduced segments, and revolved their pleura through 180°, besides directing them rearward. In this condition they strengthened the tail spine and probably collaborated with it. If, like Raasch, we were to divide the abdomen into pre- and post-abdomen, the latter should be only segment 12 and the following three reduced segments.

The appendages.—As to the appendages, if the slender evidence gathered by Raasch is reliable all that we know, is that no antennae have been seen, that an anterior pair of chelicerae of four parts appear to be present, and that behind these there are leg-like appendages beneath head and abdomen. The number under the head is apparently an assumption based on the presence of chelicerae. Raasch rules out any close relationship with the trilobites, because in his view these are Crustacea and have anten-

nae; and also they have only five pairs of cephalic appendages and, hence, less somites in the anterior body tagma. He hails with approval the statement of Clarke & Ruedemann (1912) that the trilobites cannot be ancestors of the Eurypterida. These views comprise three errors: (1) that antennae are the equivalent of chelicerae; (2) that the trilobites are crustacea; (3) that the trilobite and crustacean heads have less somites than has the chelicerate prosoma. All of these are rebutted by the writer (Raw, 1953, p. 103–111,122–127, and above). On the contrary, the very close comparisons that can be instituted between the Aglaspida and the Olenellidae indicate close relationship between the two. The great reduction of the labrum, the presence of chelicerae and the agreements with the Eurypterida indicate that Aglaspida are chelicerates. But the weakness of the whole ventral integument suggests that they have not advanced very far from the trilobite. Hence it is possible that the bulk of the appendages were still biramous as in the trilobite including possibly most or all of the abdominal appendages I–XI and probably some of those on the head. But already the primitive chelicerate modes of locomotion had been adopted, as is indicated by the points of agreement with the eurypterids. Hence, it is probable that already the head limbs behind the chelicerae were becoming specialised as walking legs and losing their gill branch; and in the abdomen the gill branch on the anterior segments in the clearest water were specialising in respiration whereas the walking leg here was being reduced; and on the hind segments the appendages were suffering atrophy.

Just as there is no reason to suppose that the "gills" or the respiratory function migrated forward, so the same applies as regards the genital organs. Raasch suggests (p. 109) that not only the gills, which he supposed migrated from a position beneath the post-ventral plate, but the genital organs, also, migrated forwards between Aglaspida and Eurypterida which he regards as doubtful descendants. Just as gills were primitively segmental, so were reproductive organs; and as is discussed under Eurypterida, so in the Aglaspida the same principles held sway. Considering how little we know of the Aglaspida and what is known of "Arachnida," Xiphosura and Eurypterida, it seems probable that already in the Aglaspida the genital function was concentrated in the front of the abdomen and the respiratory function would have ceased from the rear segments.

The aglaspid body-form.—Raasch has not realised the body-form of the Aglaspida in general, though of *Aglaspis barrandei* Hall and *Aglaspella eatoni* (Whitfield) he states that the carapace and abdomen were highly convex (p. 9,21), and of *Cyclopina vulgaris* Raasch that the shield was highly arched as indicated by specimens in sandstone (p. 34). The eight other references to body-form all express the view that in life the shield had low convexity. This was clearly not the case. The Aglaspida in general had falcate pleura, and in life the pleural spines fitted up to one another forming continuous lateral walls. It is the special function of falcate pleura to do this while offering no resistance to forward movement through the mud. In this feature they agree perfectly with the most primitive trilobites, the Paradoxidae and Olenellidae. The body-form was a semi-ellipsoid, a development from the semi-ovoid body-form which the writer has shown to be characteristic of those trilobites, and which he claimed to be characteristic of the primitive pre-Cambrian forms. Take as examples the best represented species—*Aglaspis spinifer* or *Glypharthrus thomasi* (Walter) (Raasch, pl. 1, 2,20). They are probably all entombed upside down and sedimentation has flattened them out. As claimed below, though found in marine deposits, they are derived from the beds of the fresh waters up-country, and had been swept away and carried upside down by flood waters to where they settled in still water. The load of sediment which flattened them caused folding or crumpling of the head shield, whereas in the segmented abdomen, it telescoped the axial, while it opened out the lateral parts. This is indicated by comparison of the outlines of separate tergites with their boundaries in the complete shields. The shapes of the pleura with anterior articulating areas and falcate ends adapts them to assume in life a high convex semi-ellipsoid form, within which was a water bell or hy-

dropome for respiration and with the highest and clearest water under the anterior half of the abdomen. Their normal life was thus on the bottom, where they collected their food and ploughed their way through the surface mud using for locomotion their cephalic limbs, but behind this using also their abdomen as a whole by straightening it while the tail spine acted as a fixed prop. After the head had been advanced in this way, the semi-ellipsoid form would be again assumed. But now and then they swam away upside down and relatively flat to a new site, where, after settling, the tail spine was used in turning over. To these two different modes of locomotion and body-pose one can attribute the falcate pleura and the great development of the articulating areas.

Habitat and mode of life.—Under "Distribution" Raasch discusses their geological and geographical distribution, their habitat and mode of life. They are found in Upper Cambrian marine deposits of the dominantly arenaceous St. Croixian of the Upper Mississippi basin, mostly within the west border of Wisconsin. He assumes throughout that they were marine, inhabiting the same coastal waters as the associated marine faunas (p. 88,89). He compares the Lodi (Trempealeauan) *Aglaspis* species with the modern *Limulus*, and postulates similar habits and habitat (p. 109). He thinks that aglaspids inhabited the coastal sands and that their shields and fragments were transported to the muds where they were entombed (p. 88,89).

Strong reasons can be adduced for a very different view. The creatures with which they can be most closely compared are the Eurypterida, Synxiphosura and the Xiphosura. The last named are now represented by the modern *Limulus* species, but, as was indicated first by Stromer von Reichenbach (1907), they became marine secondarily, by the inland waters to which they had been confined becoming saline owing to the aridity of Permo-Trias time, and from which they escaped to the sea. The Eurypterida were for long regarded as marine (e.g., Clarke & Ruedemann, 1912), later they were considered both fresh water and marine, but they are now acknowledged as fresh water (O'Connel, 1916; Størmer, 1934). The Synxiphosura and the Aglaspida are both very rare, and their distribution suggests a fresh water habitat. Aglaspida are limited to a narrow belt in U.S.A. with a maximum width of 400 miles. Were they marine, one would expect to find them in Europe. True, they are not found in fresh water deposits; but no Cambrian fresh water beds are known. The specimens are mostly fragments—dismembered portions of the dorsal shield. Raasch agrees that they did not live where they are found. Hence, a fresh water habitat is much easier to accept than a marine one.

As to their food, Raasch expresses the view that they were not raptorial and that their eyes had poor or no image vision, that "most aglaspids were satisfied with any inert potential food from the bottom." But chelicerates are raptorial by original nature and they probably fed, the writer thinks, mainly on the annelids which preceded them up the fresh waters, maintaining their position against the current by burrowing as did also other aquatic chelicerates. Perhaps floods dislodged them and carried them out to sea.

Phylogeny.—Though we are indebted to Raasch for an excellent descriptive account of the Aglaspida, the writer cannot commend his discussion of relationships, nor his conclusions graphically expressed by phylogenetic trees on p. 82,83, which could hardly be further removed from his own ideas (Raw, 1953, p. 122–127). Of the relationships expressed on the two pages, two can be approved, namely, that the annelids gave rise to the arthropods and that the ancestors of the Eurypterida gave rise to the scorpions.

Raasch derives the Merostomata represented by Aglaspida through the Onychophora (!) from the Annelida. He dismisses the trilobites from this descent because they are claimed as Crustacea, having antennae and also comprising less segments in their anterior tagma. His view is partly based on the erroneous belief that chelicerae represent antennae. The writer on the contrary derives the aglaspids directly from pre-Cambrian ancestors of the Olenellidae (as need not be repeated here), and he claims the cephalic tagma as having the same constitution in all true arthropods, and that,

in all, the antennal "segment" is in front of six other normal segments.

With this order can also be associated the much later *Pseudoniscus* (Clarke, 1901) and *Weinbergina* (Richter, R. and E., 1929). Both of these may well be direct descendants: they display 10 segments only between the head shield and the tail spine indicating that before their dates in the Upper Silurian and Lower Devonian, the anterior tergite had disappeared from sight (or almost so in *Weinbergina*) as a result of the specialisation of the limbs, the first abdominal pair having migrated forward under the head to close the mouth space behind.

The evolution of this group was parallel to that of the Eurypterida, and they had the same ancestor; but at the divergence the axial spine of the macrosomite which determined the effective termination of the body was in their case the one next in front (three somites in front) of that which formed the tail spine of *Olenellus* and the eurypterid and the sting of the scorpion.

From the Aglaspida Raasch derives the Beckwithida reviewed below and from these the Xiphosura.

Order BECKWITHIDA, n. order

Beckwithia typa Resser was described by Resser (1931) as a new genus and species, and was compared with *Aglaspella* ("*Aglaspis*") *eatoni* (Whitfield). (See also Raasch, 1939, p. 46, pl. 19.) It comes from the Marjum formation of Weeks Canyon, House Range, Utah, referred to the top of the Middle Cambrian.

Though the only specimen known, the dorsal shield is complete and like the previous order it is of special interest in this study. It differs from the Aglaspida much as different genera of the Olenellidae differ from one another. If, with Raasch, we define the Aglaspida as having beneath the post-abdomen the ventrally facing "post-ventral plate," we must separate *Beckwithia* from them. Also, whereas aglaspids have 11 free segments and bear the tail spine on the 12th, *Beckwithia* has 8 free segments and bears the spine on the 9th which is part of an extensive pygidium. A separate order is therefore suggested for it.

Characteristics and segmentation.—The specimen exhibits its dorsal surface. It is complete except for the broken off tail spine; but it has been disturbed, so that the head is turned round upon the abdomen through about 20°. It is peculiar for bearing upon its surface five attached valves of *Obolus johni* Resser, so that, if these attached themselves after the death of the animal, it was entombed as in life. Resser's description is very complete. As flattened out, the shield is ovate, being twice as long as broad, and with greatest width at the genal angles of the cephalon. In life it must have been greatly arched: the wrinkling of the cephalon and the spacing of the post-cephalic segments indicate the extent of the flattening.

The head agrees with the Aglaspida. The main area is coarsely pustulose, the pustules diminishing towards the flattened rim. The distance between the eyes is a third the width at the genal angles, and the distance of each from the middle of the front edge is the same: they are described as ovate or crescentic. The rear boundary of the head is wavy as in *Aglaspis spinifer*, but more so.

In the abdomen the eight free segments repeat the form of the rear of the head, but successive pleura are directed more and more to the rear, so that their ends are well separated. The pleural spines are truncated —falcate.

The pygidium measures two-fifths of the abdomen in front. It is pentagonal, the three anterior sides fitting the segment in front and the angle between the posterior sides being rounded. It bears an axial spine, not at the rear, but "a little forward of the center and extends upward and backward" and "must have projected beyond the rear margin." The tergites of its segments are completely coalesced, so that no segmentation is visible.

The third abdominal segment bears a short axial spine and there is a slight suggestion, too, that the sixth may also have borne one, but the particular area is covered by a specimen of *Obolus*. Which segment bears the tail spine might be in doubt; but as its base begins about the length of a segment behind the front of the pygidium, and seeing that triadic merocyclism has such an important control of segmental features in chelicerates, it is here claimed to belong to the 9th segment, a macrosomite like the

3rd, 6th and 12th. The number of segments in the pygidium cannot be seen, but again since triadic merocyclism controlled, it is probably four ending in the 12th, a macrosomite. This is quite in harmony with its size if we allow a small reduction of length to its segments. Whether the secondary anus was beneath the 9th or the 12th cannot be stated; but the 12th seems more probable.

With the tail spine on the 9th instead of the 12th the body-form is relatively shorter than in Aglaspida, and, in view of the contrast between cephalon and pygidium, was a semi-ovoid.

Størmer in his figure (1944, p. 75, fig. 14, no. 15) furnishes *Beckwithia typa* with a hypothetical tail spine at the extreme rear of the pygidium in addition to the one already noted. There is a slight suggestion in the photograph that this may be the case. Should this be so, its evolution would be easier to envisage. In any case we can confidently picture an earlier stage, when the axial spines of the macrosomites were more equal. Then after the adoption of the olenellid-chelicerate mode of life, a posterior one or two (9th and 12th) axial spines developed while the rest diminished. But there were great divergencies, and the evolution which led to *Beckwithia* is in marked contrast with that of Aglaspida; for in it the body ends with the 12th abdominal, and none are specially reduced, for the last four do not contrast with the others except by coalescence. This results probably from the use of these segments and the great axial spines on 9th and 12th in exerting a posterior push, when, in locomotion, the previously arched abdomen was straightened.

Phylogeny.—Raasch derives *Beckwithia* from the Aglaspida, and he also derives the Xiphosura from it. But neither is possible: no aglaspid that he describes could give rise to it, for all have lost all axial spines except that on the 12th abdominal segment. Both orders are derived from a common, more generalised, ancestor.

Størmer includes in his Xiphosura both these orders as well as the Synxiphosura and derives it from *Olenellus*, not withstanding the varying numbers of segments in front of the tail spine. However, if one widens the Xiphosura so as to include these, why not include also the Eurypterida?

The writer would suggest that both *Weinbergina* (Richter, R. and E, 1929) and *Pseudoniscus* (Schmidt, 1883, pl. 1, fig. 48, p. 40; Clarke, 1901) may be direct descendants of Cambrian Aglaspida. The first is Devonian, the second Silurian: both have 10 evident segments between the cephalon and the tail spine, and it seems probable that since Cambrian time the first tergite has gone out of sight with the forward advance of the first-abdominal appendages to serve the mouth, as stated above.

Synxiphosura

The extreme rarity and local occurrence of these fossils besides their occasional presence in fresh water deposits indicate their fresh water habitat. Their rarity is partly responsible for our very limited knowledge of them. Two genera are sufficiently known and are best represented by the following:

Hemiaspis limuloides H. Woodward from the Lower Ludlow (Upper Silurian) (Woodward, 1866–78, p. 174, pl. 30, fig. 1), and reproduced abundantly elsewhere.

Bunodes lunula Eichwald from the Upper Silurian (Schmidt, 1883, p. 43, pl. 7, fig. 1–6). This has been restored by Størmer (1934, p. 9, fig. 1b).

These much resemble one another, and in both we have a semicircular cephalon on which the radiating positions of the underlying limbs is suggested. Behind this the abdomen is subdivided into three tagmata, a pre-abdomen of seven evident segments (6 and 7 being coalesced) but showing their pleura, a post-abdomen of three ring-form segments and a pointed tail-spine.

As both of these are Upper Silurian, it is here suggested that an anterior tergite has disappeared in both as in eurypterids and scorpions with the forward movement of its appendages to serve the mouth. This would make the tail-spine the 12th somite, a macrosomite. Størmer (1934, fig. 2) makes it the 11th, but he also makes the tail-spine of *Limulus* the 11th.

The Aglaspida and the Synxiphosura end in a tail-spine. No "Arachnid" except the scorpion does this: in them the last significant segment is an ordinary one, which

suggests that it was not the axial spine but other features of the macrosomite that made it end the body. Further, the abdominal segmentation of the best preserved Aglaspida has above been deduced as 12+3 reduced.

Though no arachnid agrees with this exactly, the Thelyphonida and Schizomida have 9+3 reduced+flagellum (or n greatly reduced) and the Phrynychida has 9+3; the Pseudoscorpiones, Araneae and Solifugae have 12 or 11. The 11 might be due to coalescence of the last two normal segments due to wielding a flagellum which may subsequently have been lost.

7. CHELICERATES WITH 9 SIGNIFICANT POST-CEPHALIC SOMITES—XIPHOSURA

Text-fig. 9C

The segmentation of the Xiphosura is still in doubt. Lankester (1910–11) gives the abdominal segments as "not more than 10 ending in post-anal spine." Petrunkevitch (1947), after discussing the segmentation of the prosoma, says of the abdomen that the chilarial or 1st segment apart from its pleura "is restricted on the dorsal surface to a small lens-shaped area of soft membrane between the two shields." The genital segment embraces the adjoining parts of the abdominal shield and the first pair of moveable pleural spines. Behind this the shield is made by the five gill-bearing segments, which embrace also the other five pairs of moveable spines. He says

> The rest of the abdomen shows no trace of segmentation even in the embryo. Whether it represents five somites bringing the total number of abdominal somites to 12 as in Arachnida must be left unanswered at the present state of our knowledge.

Of the chilaria he states also that "they have no homologous counterpart in Arachnida."

But we can go further: first, with Lankester (1910) and with Vachon (1949, p. 390), we can accept the sternum of the scorpion as these "counterparts," and so also the metastoma of the eurypterids. And now that we have in merocyclism a mode of origin of a variety of numbers of abdominal segments in the chelicerates ranging from 15 to 6, we can select the trilobite stage of the king crab's ontogeny, in which the segmentation is most clearly marked. This suggests only one segment between the last pair of moveable pleural spines and the tail spine, which give us nine abdominal segments, no. 1 being the chilarial and no. 9 the tail spine. There is no telson, the anus being secondary. This conclusion is supported by the work of Patten & Redenbaugh (1899) on the nervous system of *Limulus*. Behind the six nerves to the genital segment and the five gill segments one only goes to the rear angle of the abdominal shield before issue of the nerves to the tail spine. The greater length of this segment over those in front is attributable to the great development of the muscles moving the tail spine. If one adds to these the nerves to the pre-genital segment, this gives a total of nine abdominal nerve pairs and so nine segments.

The same conclusion follows from the study of the clearly related but more primitive Carboniferous and Devonian belinurids, in which the pleura were still free, and the segmentation was still primitive and clear, suggesting eight segments in front of the tail spine, which, as it is not a telson, is the 9th post-cephalic segment. In the latest of these, such as *Prestwichianella* and *Euproops*, the first segment may not be visible through its extensive slipping under the head shield in furnishing the homologues of the chilaria to it.

Størmer (1944, p. 66,67) accepts the views of Iwanov that the distribution of the segments in *Limulus* is very peculiar, that indeed the hinge between the prosoma and the abdomen is not and was not a segmental boundary, but that it lies between the mestotergites of VII and VIII and laterally cuts across the pleurotergite VI. This latter view he imports also into his interpretation of the trilobite, where in all cases the rear of the cephalon, he claims, *is not a segmental boundary* (1942, p. 145, 158)! This the writer cannot accept: any peculiarity of *Limulus* at this junction is attributable to the migration and reduction of segment VII, the mesotergite of which has extensively slipped under the prosoma, whereas the pleura, though reduced, are still part of the abdomen forming angulated raised anterolateral areas. In the prosoma, the specialisation is so great that it

may not be possible as yet to indicate the distribution of the segments, though Petrunkevitch (1947c, fig. 1,2) has attempted it, and the writer fully accepts this as regards the abdomen.

Størmer also discusses the ontogeny and phylogeny of the Xiphosura, but reaches conclusions very different from those expressed above. He derives them from *Olenellus* through the Aglaspida and the Synxiphosura, but makes no suggestion as to how the tail spine changed from the 15th post-cephalic to the 11th as he claims. Following Iwanov (1933), he shifts the trilobite stage in the ontogeny of *Limulus* back to an early embryonic stage (Størmer, 1934, p. 7–11; 1944, p. 75–79, 114–116; 1952). Some of Iwanov's conclusions cannot be accepted; for example, he claims that the protaspis of the trilobite bore besides antennae, four pairs of feet which were homologues of the *first* four pairs of appendages of the Xiphosura, and that in the evolution of this from the trilobite there were added somites V, VI and VII, the last adding also the chilaria to the chelicerate prosoma. Here, on the contrary, it is claimed that the protaspis and the head of the trilobite embraced somites I–VI of the chelicerate prosoma, besides bearing antennae from a "somite in front." Iwanov assumes (1933, p. 321) that the homologues of crustacean antennae as well as antennules are wanting from the prosoma. The three somites added to the trilobite head in the evolution of the Xiphosure he sees in the first three segments of the thorax of *Olenellus vermontana* (p. 324). In the writer's view so much of Iwanov's conclusions are wrong, as to throw doubt on his embryological results.

Potts (Borradaile & Potts, 1935, 1941, p. 529) pointed out that *Hemiaspis* and *Bunodes* have three reduced segments before their short caudal spines and concluded that the tail of the king crab had been formed at the expense of the reduced segments; but Potts would not know the Olenellidae.

The nervous system of *Limulus* has lately been investigated by Henry (1950). She had dissected the prosomatic part of the central nervous system in no less than six successive stages ranging from the embryonic "trilobite larva" up to the adult. Her dorsal view of this in the trilobite stage, which naturally is the most primitive, exhibits from front to rear what were recognized as protocerebrum (innervating the eyes and frontal organs), deutocerebrum (without appendages but corresponding with the trilobite antennae), tritocerebrum (innervating the chelicerae and giving origin to the visceral nervous system) and the five pairs of ganglia innervating the five pairs of legs. All these eight pairs succeed one another and occupy approximately equal lengths. In agreement with the views above expressed they can be interpreted as corresponding with the successive components of the trilobite's head and as pointing back to the polychaet—the protocerebrum coming from the polychaet brain in the prostomium, the deutocerebrum from the next pair of ganglia innervating the trilobite antennae, the tritocerebrum (innervating the chelicerae) together with the following five pairs of ganglia corresponding to the six normal segments of the trilobite's head. However, as Henry was straining to support Ferris's theory of the segmentation in the annulata, she attributes the first two to segment 3, the next with the chelicerae to segment 1, and the other five to segments 4 to 8. Of her segment 3 she states (p. 130)

> There are no nerves from the ventral neve cord which can be ascribed to segment 3 . . . this segment has been taken over by the head lobe and all the structures which it bears are innervated from the dorsal cerebral ganglion.

Of the tritocerebrum she states (p. 129)

> This is generally conceded to be the first ganglion of the ventral nerve cord and to bear the connection with the stomodeal nervous system. It is here also held to be . . . the ventral ganglion of the morphologically first segment of the body . . . of the prostomium of Oligochaeta and the labrum of Crustacea and insets.

On the contrary, in the writer's view the labrum in all these classes originally housed and was innervated by the proto-cerebrum, and is only secondarily innervated by the tritocerebrum, as is suggested by its actual meagre innervation by the labral nerve from the middle of the stomodeal bridge. Its original ganglia went forward with the migration of the prostomial eyes on to the dorsum. In some other respects, too, her views could hardly be further removed

from the writer's, e.g., "The chelicerae" she states "seem to be homologous" . . . "with the antennae of insects and with some one of the pairs of head tentacles of the polychaeta."

In some respects, however, she fully supports the writer who in 1925 claimed that in Olenellidae the pleural spines of the first normal segment had revolved to the rear to constitute the genal spines, and that on the ventrum the rostrum also had been stretched out to the same extent and constitutes the doublure. Both of these areas are included in the representation of her segment 3 (compare her fig. 69 with Text-fig. 2D of this paper). In this she confirms in a descendant the distribution of the segments claimed for a relation of its ancestor and she corrects Patten & Redenbaugh, who considered that the nerves extended into the abdomen.

It is of interest that the kingcrab, because it has remained aquatic, has retained compound eyes, which all known aquatic chelicerates have possessed.

In still another respect the kingcrabs are of particular interest. Pleura are appendages primitively moved by muscles, and the pleural spines are their earliest and most primitive parts. In this restricted order, which has survived from the Permian period, six pairs of pleural spines alone continue moveable, while the rest of the pleura have coalesced into a rigid shield over the genital and respiratory organs.

This number nine of significant abdominal segments in the xiphosure, while it does not fit in with the theory of Petrunkevitch that 12 is primitive, can be claimed to be well represented in the Arachnida, e.g., the Thelyphonida and Schizomida (9+3 reduced+n greatly reduced), and, possibly derived from this segmentation, that of Palpigradi (8+3 reduced+n greatly reduced), and of Phrynychida (9+3 somewhat reduced). Also in the Opiliones nine may be the number of significant abdominal segments, as also in several fossil groups—Architarbi, Anthracomarti, Trigonotarbi (Palaeocarinidae, Anthracosironidae, Eophrynidae, Trigonomartidae, a few of which have greatly reduced segments behind the nine).

With (1904) described a new suborder of Acari with nine abdominal segments, in character a diminutive *Opilion*, so this suborder of Acari (suborder Notostigmata, family Opilioacaridae) falls here (Vitzthum, 1931, p. 1)!

In some arachnids 10 segments have been claimed, but it will perhaps be found that the anus has been counted as indicating one. It never indicates a segment, and on the view above expressed, it does not in the chelicerate even indicate a telson.

8. CHELICERATES WITH 6 POST-CEPHALIC (OR "ABDOMINAL") SOMITES

Text-fig. 9D,9E

Under this heading we may consider the Acari comprising the mites and ticks, in general the smallest of the Arachnida, as well as some other groups.

Acari

Those who have specialized in the study of this order have for the most part avoided any estimate of the abdominal segmentation, i.e. that behind the homologues of the arachnid appendages; but one sub-order mentioned above [the Notostigmata (Opilioacaridae)] has an abdomen of nine segments defined by integumental grooves.

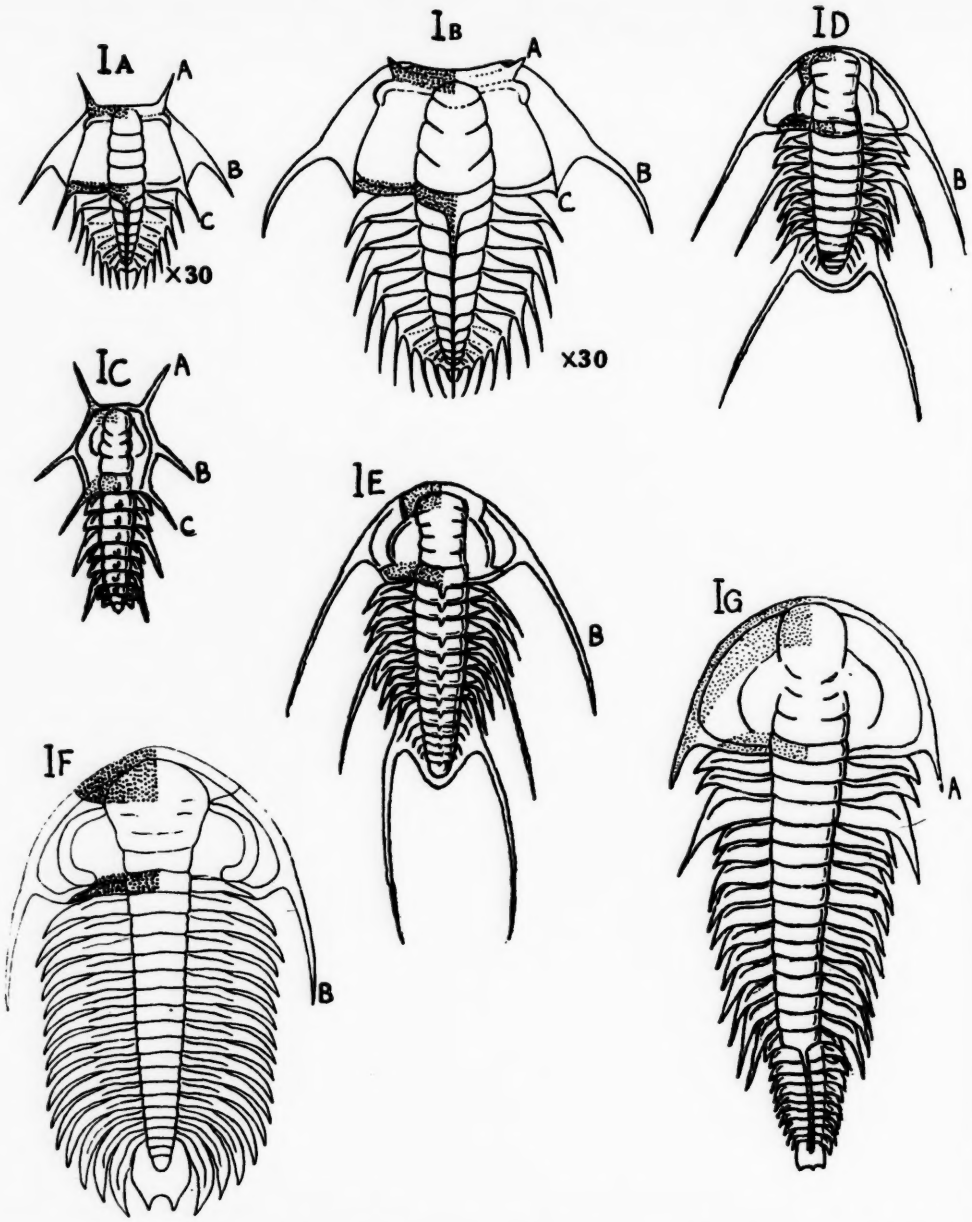
Though Lamarck regarded the Acari as primitive, later writers have accounted them degenerate, as is suggested by their usually minute size and their frequent parasitic mode of life.

In one of the latest works André (1949, p. 794) states

> The Acari do not constitute a natural ensemble, but comprise several heterogeneous groups derived from phylogenetically distinct lines. Their metamery is strongly degraded; and in the rare cases where vestiges of segmentation are preserved, these with some exceptions do not correspond at all to that of other arachnids.

He himself avoids all discussion of their segmentation.

The characteristics of the post-cephalic or abdominal region strongly suggest that the primitive segmentation has been extensively suppressed; but suggestions of it survive in the ticks or Ixodoidea as well as in the Opilioacaridae. The Ixodidae are very constant in this suggestion of segmentation. Behind the pair of spiracles, which are associated by zoologists with the 4th pair of



TEXT-FIG. *1*—Primitive Cambrian trilobites. The anterior and posterior dorsal segments of the head are indicated by shading. On the figures A is the procranidial spine, accounted the pleural spine of the first dorsal segment; B is the parial spine, the coalesced spines of the third and fourth, and C is the metacranidial, that of the sixth or last.

A,B—Stages of development of *Leptoplastus salteri* Callaway, basal Ordovician. *A*, meraspid degree 1, *B*, degree 5; both are heptacicephalic, but in *B*, the pro- and metacranidial spines are reduced; the anterior glabellar furrow has been lost.

C—The aberrant Lower Cambrian olenellid, *Olenelloides armatus* Peach with triadic merocyclism behind the head as in *D* and *G*.

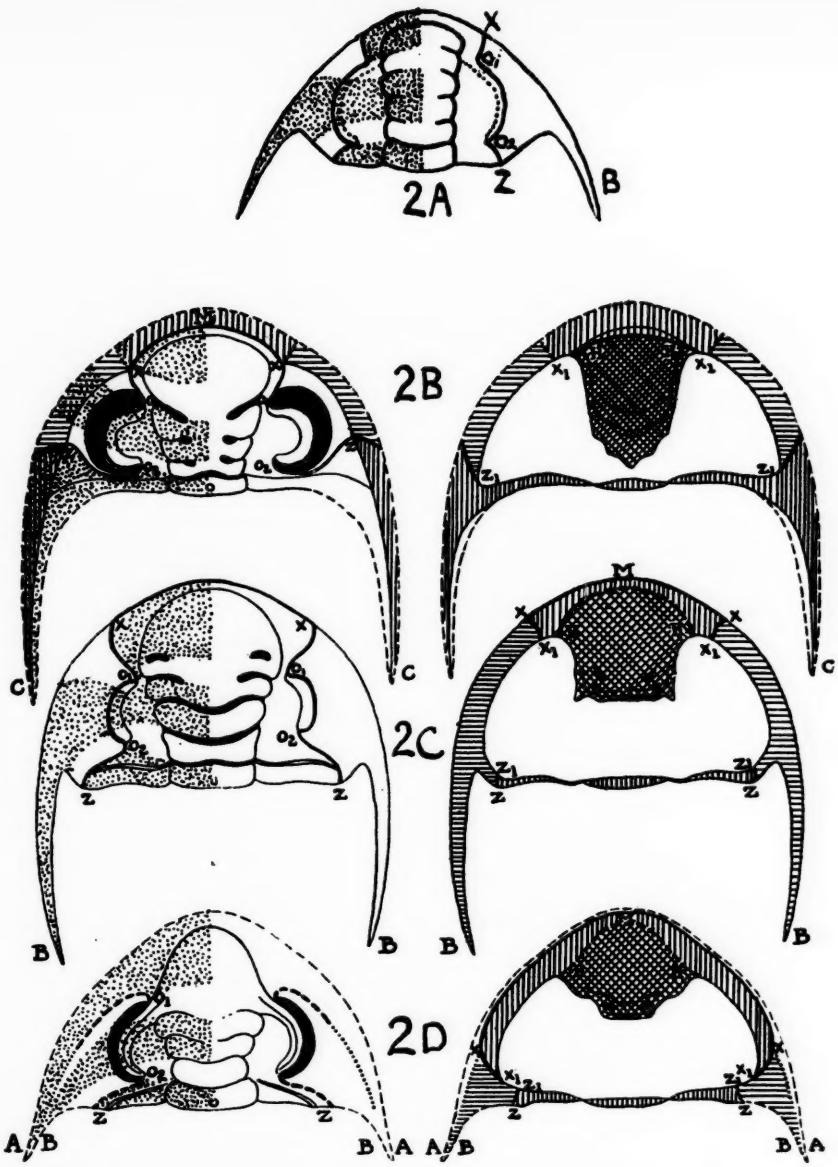
D—*Albertella helena* Walcott, Middle Cambrian.

E—*Albertella bosworthi* Walcott, Middle Cambrian, primitive by long eye and the position of parial spine.

F—*Paradoxides rugulosus* Corda, with long eye and falcate pleura of the semi-ovoid body-form.

G—*Olenellus vermontanus* (Hall). Its triadic merocyclism behind the head is indicated by post-cephalic segments 3, 6 and 15. Its body-form and pleura are a reversion.

These figures are copied from Raw, 1953, fig. 2,3, where references are given.



TEXT-FIG. *2*—Primitive proparial, mesoparial and metaparial trilobite cephala indicating the disposition of the segments, which is indicated on the left by dot-shading the dorsal areas of the macrosomites (dorsal segments 1, 3, 4 and 6), and on the primitive ventrum by cross-hatching the hypostome, vertically lining the rostrum in front and the doublure of the last segment behind, and horizontally lining the "free" cheeks.

A—Mesoparial cephalon of ***Albertella helena*** Walcott, dorsum.

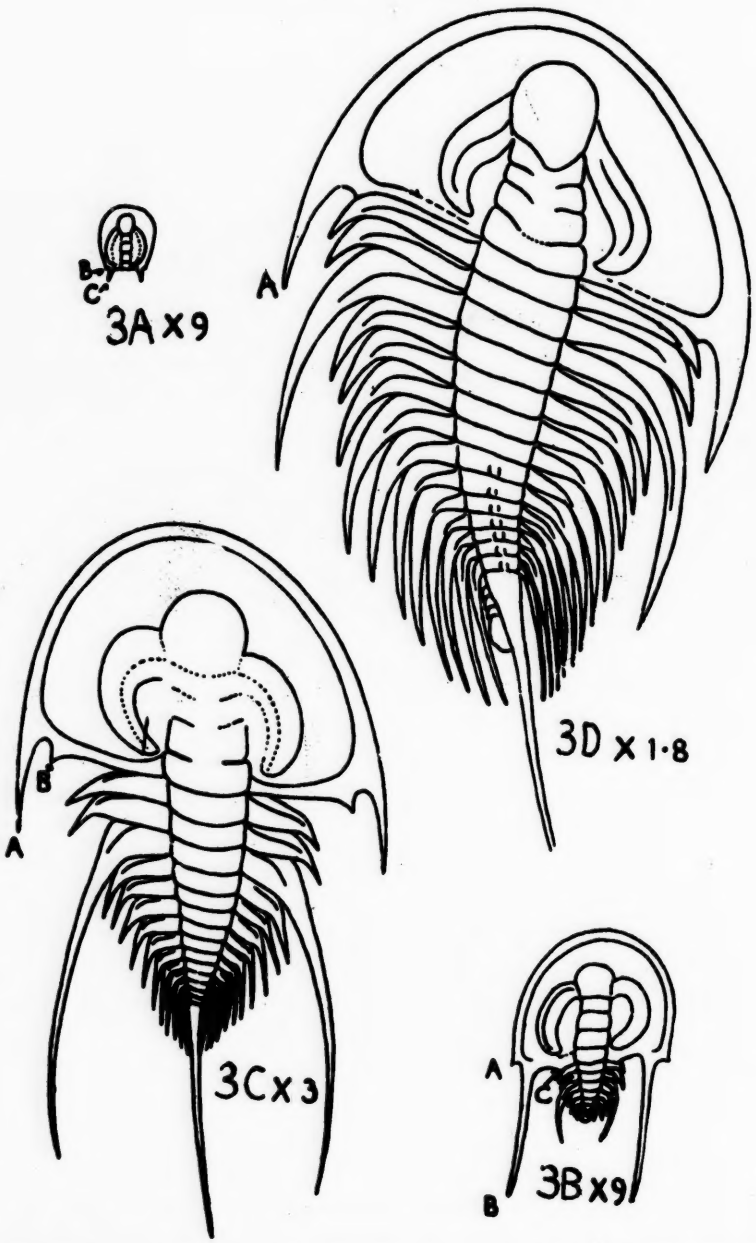
B—The proparial ***Dalmanitina hausmanni*** Brongniart, after Barrande, dorsum and ventrum.

C—The mesoparial ***Paradoxides spinosus*** Boeck, dorsum and ventrum.

D—The metaparial ***Kjerulfia lata*** Kiaer, dorsum and ventrum, both modified after Kiaer. See also Text-fig. 1C, G. In these, all of them Olenellidae, ankylosis has taken place along the facial sutures.

On all figures A = procranidial spines, X = loci of their bases when these are absent; B = parial spines, C = metacranidial spines, Z = loci of their bases, when absent. HH = hypostomal suture, XMX = rostral suture, XO_1O_2Z = dorsal facial suture, but these are ankylosed in metaparial trilobites. XX = connecting sutures, ankylosed in 2B. ZZ = posterior ventral sutures, ankylosed in metaparial trilobites, e.g., *2D*.

All from Raw, 1925, pl. 15.



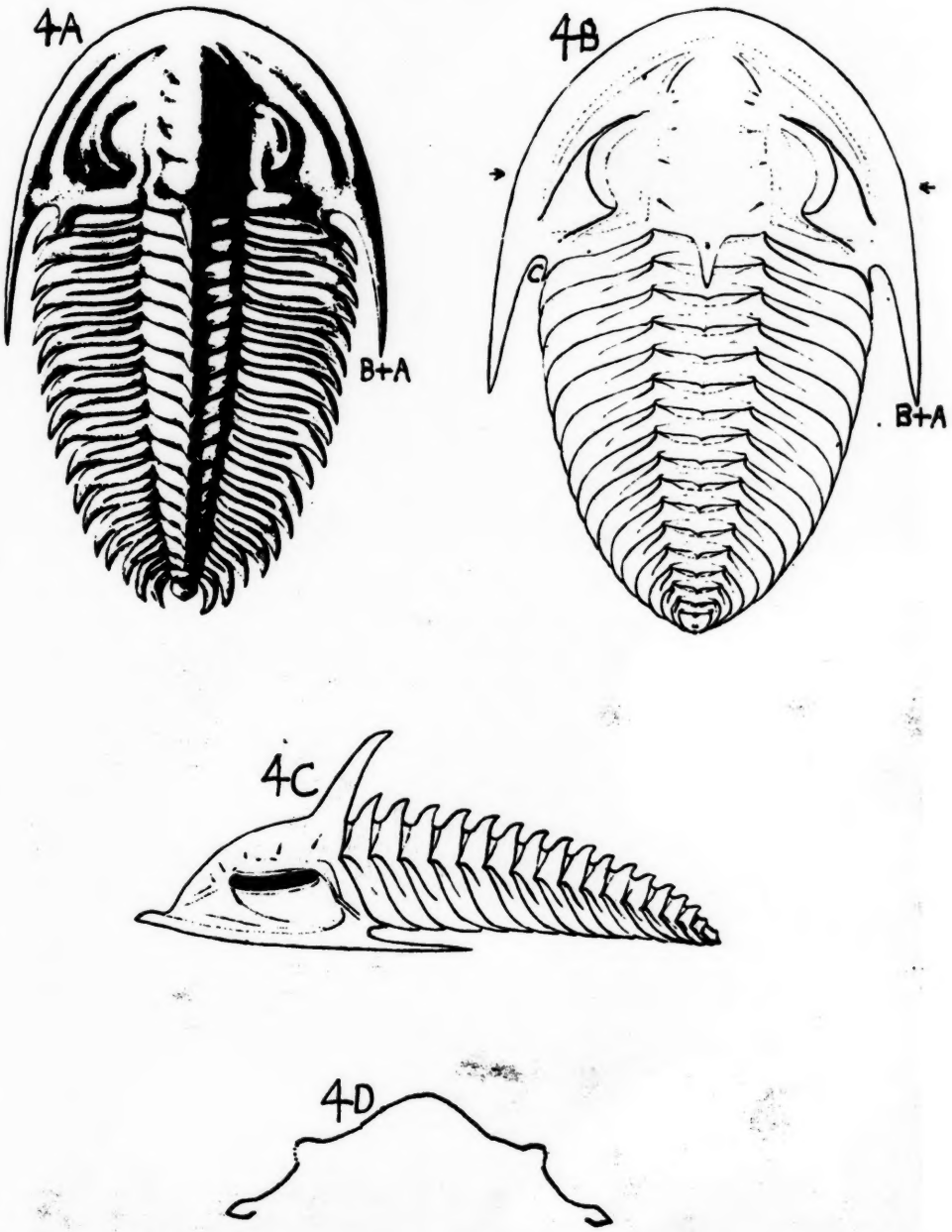
TEXT-FIG. *3*—The ontogeny of an olenellid, *Paedumias yorkense* Resser & Howell (Walcott 1910, pl. 32; Resser & Howell, 1938, p. 227).

A—A protaspis with the metacranidial spine C dominant.

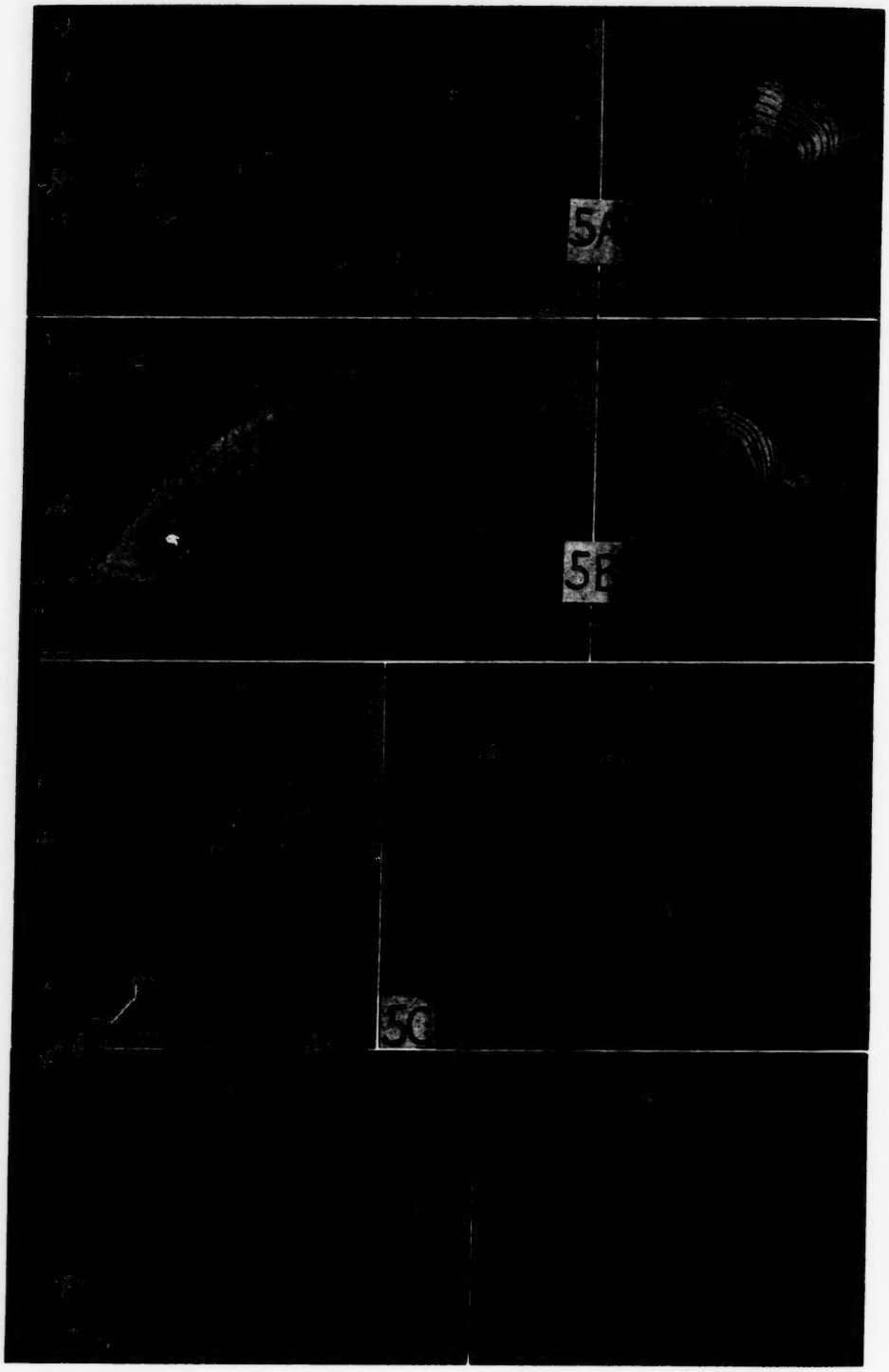
B—An early meraspid stage with the parial spine B dominant.

C,D—Early and late holaspid stages with the procranidial spine A dominant. The tailspine on the 15th post-cranidial segment is followed by three reduced segments and a little pygidium.

All from Raw, 1927, p. 142,243; after Walcott, 1910, pl. 32.



TEXT-FIG. *4*—*Callavia callavei* (Lapworth), an olenellid trilobite illustrating the semi-ovoid body-form.
A—Lapworth's restoration, represented as flattened (Lapworth, 1891, pl. 15).
B—Raw's restoration as a semi-ovoid.
C—Same, side view (Raw, 1953, fig. 6,).
D—Same, cross section of head.



TEXT-FIG. 5—Models of olenellids cut in thin card and bent till the pleural spines fit one another. It is not possible to bend the flattened head into a quarter-sphere nor to telescope the axis, so the semi-ovoid is only suggested.

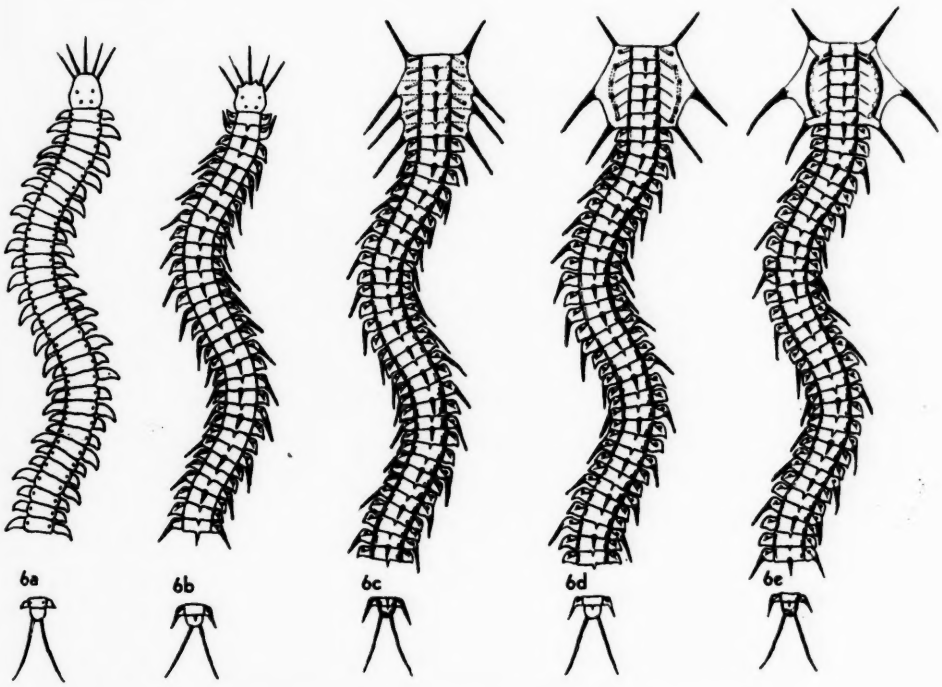
A—Elliptocephala asaphoides Emmons, side and rear views (Walcott, 1910, pl. 24).

B—Olenellus thompsoni Hall, side and rear views (Walcott, 1910, pl. 35). The reduced segments behind the tail-spine are not represented.

C—Nevadia weeksi Walcott, dorsal, front, side and rear views (Walcott, 1910, pl. 23).

legs, the posterior semi-circular margin is in all radially subdivided into eleven subequal parts. They remind one of the way in which the pygidium of a trilobite is subdivided by the pleura of the segments. If the median division stands alone, this would suggest six segments; and the important role of triadic merocyclism favors this. Unfortunately the suggestions of segmentation in the Argasidae, the other family in the Ixodoidea, are not quite so definite, but the radial distribution of the "discs" and of the intestinal caeca suggest about the same number (see Nuttall et al., 1908, 1911, 1915; Robinson, 1926). In both trilobite and acarine the radial distributions can be attributed to the shortening of the body of arthropods whose segments bear pleura.

Since this paper was written, Snodgrass's Textbook of Arthropod Anatomy (1952), comes to hand. He takes the tick *Dermacentor variabilis* (Say.) as one of his types



TEXT-FIG. 6—Stages in the evolution of the arthropod suggested by the trilobite.

A—A hypothetical polychaet combining characters of the Eunicidae, Phyllodocidae and Polynoidae (sub families Polynoinae and Hermioninae), the merocycles being diads to segment 23 (normal segment 22) and triads behind. Segmental eyes are represented on terga.

B—The pro-arthropod, annelid-like in segmentation, but the terga protected by stronger cuticle and by axial spines as well.

C—The prot-arthropod, first stage. The segmental eyes have moved on the pleura. The prostomium and peristome are subretroverted, and the first six normal segments combine with them to form the head.

D—The prot-arthropod, second stage. The adjoining pleural spines on macrosomites 3 and 4 have coalesced into the parial spines making the head (with the occipital spine) heptacicephalic. The six dorsal eyes on each cheek are enlarged, and are becoming innervated by the nerve to the first. These lines of eyes continue to be lines of soft cuticle and, with the soft interpleural lines behind the first or procranidial pleura and in front of the last or metacranidial, become the dorsal facial sutures of the trilobite.

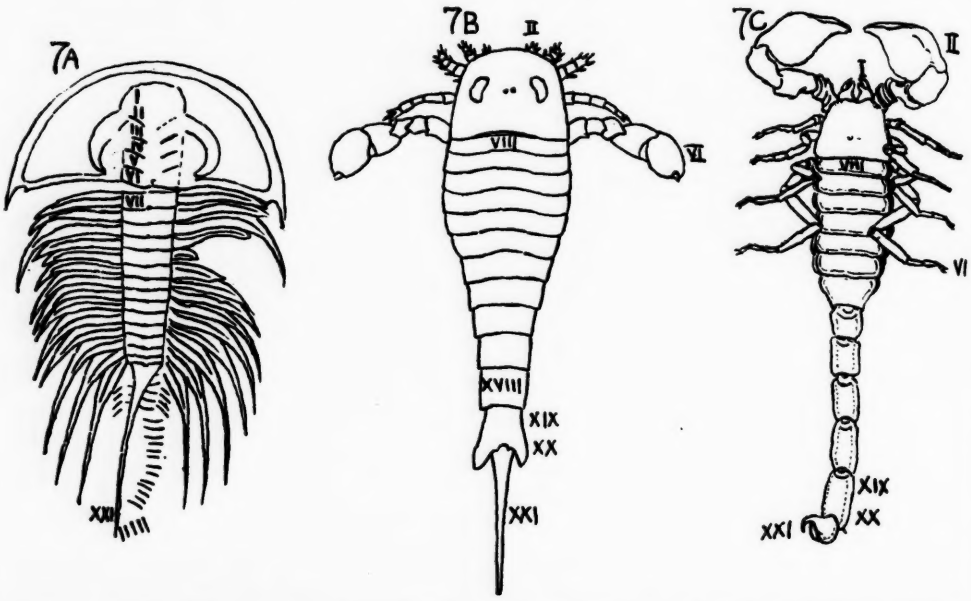
E—The deut-arthropod, with compound eyes. These radiate eyes have developed along the common optic nerves. Perhaps all arthropods have these eyes in their ancestry, for the arachnids have lost them. In the deut-arthropod stage represented, the triadic merocycles have moved forward up to the head. These are the ancestors of the Trilobita, Arachnida, Crustacea and Insecta.

and though he does not claim the festoons as so many segments, he regards the genital grooves on the venter as indicating the distribution of the genital or 2nd abdominal segment, saying

> it is probable that the abdominal sterna have been extended forward between the legs, and that the gonopore is really on segment VIII as in other arachnids. The anus lies at about the centre of the abdominal region of the tick, but, as with the spiders, its position represents the posterior pole of the body.

All this can be fully accepted, and the distribution of the six abdominal segments is thereby approximately indicated.

It has above been deduced that the chelicerates have been derived from an unknown, pre-Cambrian, metaparial trilobite characterized, like the ancestor of the Olenellidae, by triadic merocyclism. The number (6) of abdominal segments which are suggested by the ticks embraces two such merocycles, each of which would end in a macrosomite. It is accordingly suggested that just as there was a living to be made by chelicerates with only 15, 12, or 9 significant post-cephalic segments, so also there were places in nature for chelicerates with still smaller abdomens, indeed with only 6 and perhaps with only 3 or none of these segments. It is suggested therefore that forms arose which had no use for more than 6, and possibly others with no use for more than 3 of postcephalic segments, behind which the rest failed to be developed; and that in this way were originated the ticks and mites. But besides beginning as relatively small aquatic creatures there will have been an evolution of minuteness to fill the special niches for dwarfs after their invasion of the land, as would seem to have occurred also in the evolution of the insects.



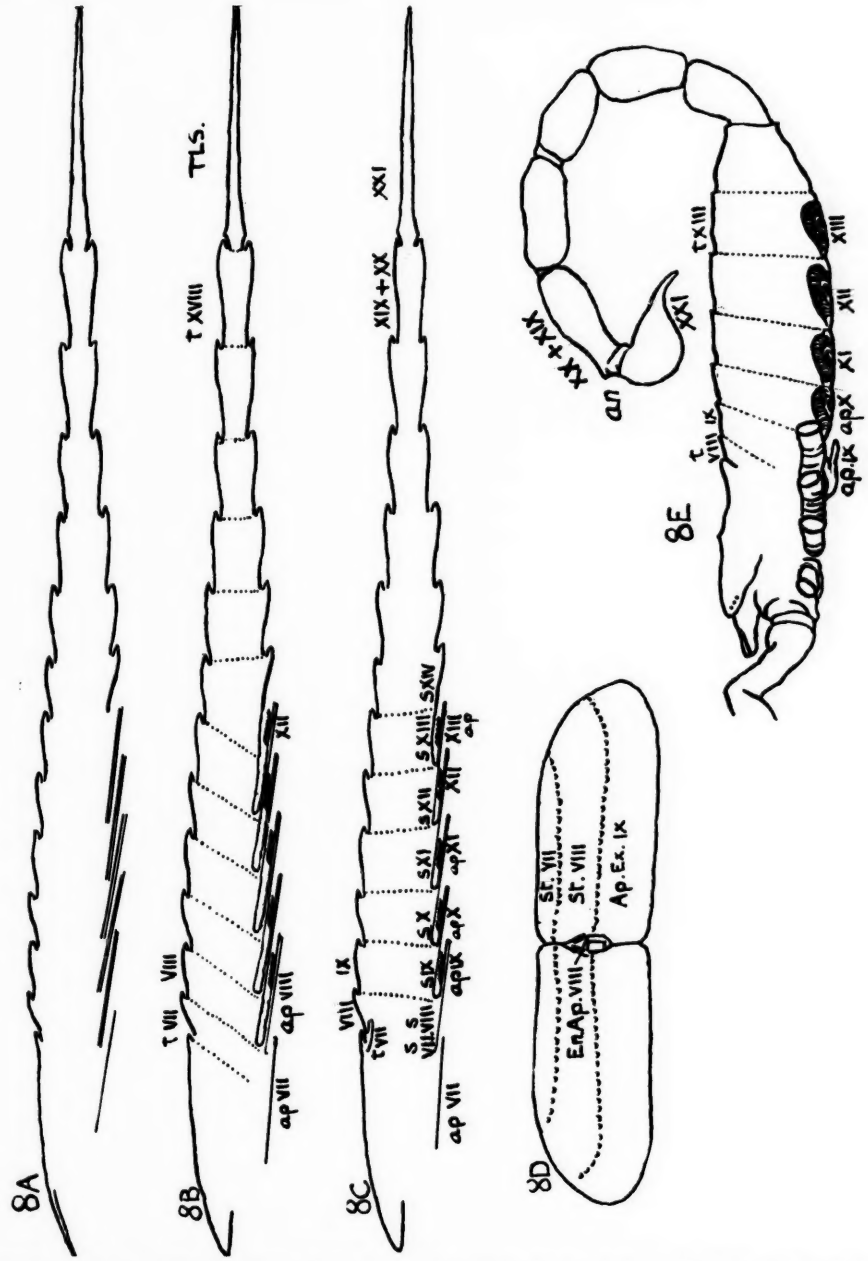
TEXT-FIG. 7—Dorsal surfaces of *Olenellus*, *Eurypterus* and *Scorpio*, all with the same primitive segmentation as here suggested.

A—The mutilated *Olenellus robsonensis* (Burling) after Burling's photograph (Burling, 1916, pl. 1). It is selected because it shows at least 19 reduced segments behind the tail spine, without reaching the end of the body. The first and last significant post-cephalic segments are numbered VII and XXI, but the reduced segments behind are greatly disturbed and are only indicated by the boundaries of the axial parts.

B—*Eurypterus fischeri* Eichwald, after Holm.

C—*Scorpio swammerdami*, copied from Shipley and MacBride's Zoology.

In both *Eurypterus* and *Scorpio* the first tergite is VIII and the last before the tail-spine and sting is composite.



TEXT-FIG. 8—Longitudinal sections through one side of the body of *Eurypterus fischeri* Eichwald to illustrate the views (*A*) of Schmidt and Holm; (*B*) of Størmer and Petrunkevitch; (*C*) of Raw. (*D*) the so-called "operculum" of the same, (*E*) longitudinal diagram of *Scorpio* with abdominal segments and appendages.

A—Schmidt's section (1883) pl. 3a, fig. 1c): Dorsum—behind the carapace are 12 terga and the tail-spine. Ventrum—beneath the posterior half of the carapace is the metastome, a single line *here*, behind which are 5 overlapping pairs of lines representing the "leaf-feet." Holm did not replace this

(*Continued on page 188*)

Indeed Nature's call for dwarfs will explain minuteness effected in other ways than by merocyclism, e.g., the Opilioacaridae.

Ricinulei

Still another arachnid order falls to be mentioned here, the Ricinulei; only known at all since 1838, it is 50 years since Hansen & Sorensen (1904) first claimed their distinctness and instituted the ordinal name. It is a truly extraordinary order, on which there is fair agreement. The significant abdominal segments are 6; 6,+3 greatly reduced and telescoped (Hansen & Sorensen, 1904; Petrunkevitch, 1949). But, perhaps stimulated by the endeavour to see 12, Kästner (1932, 1940) gave 7+3 reduced and Millot (1949) gives 7+4 reduced. The Ricinulei are remarkable in many ways: for their small size, the large size of segments 4–6 compared with the rest, the strength of the cuticle and their possession of a unique body member, the cucullus. Comparison with their ancestor, the trilobite, suggests that this organ is homologous with the hypostome or labrum. If so, the chelicerae covered by it are here in a more primitive relationship than in the other chelicerates, and it would indicate the extreme antiquity of the order. Lastly their fossil occurrences suggest that these dwarfs were more abundant in Paleozoic time.

9. PANTOPODA

In this connection it is appropriate also to mention here the Pantopoda or Pycnogonida, for the inclusion of which among the chelicerates reasons have been given above. Seeing that so many of them have only four equal ambulatory legs besides apparent homologues of chelicerae and ?pedipalps, and that in the early evolution of the chelicerates the appendages of the post-cephalic (or "abdominal") segments lost all their primitive ambulatory functions, the suggestions made above (Section 2) to account for the ovigerous legs and the extra walking legs of the Decolopodidae still seem the best that can be offered.

From what we know of the occurrence of chelicerates and trilobites in the geological record, it is very probable that these groups with very few post-cephalic segments arose, like the others, before Cambrian time. They have thus had an enormous period in which to evolve, which is estimated at over 500 million years. This would help to account for the extreme specialization which they exhibit.

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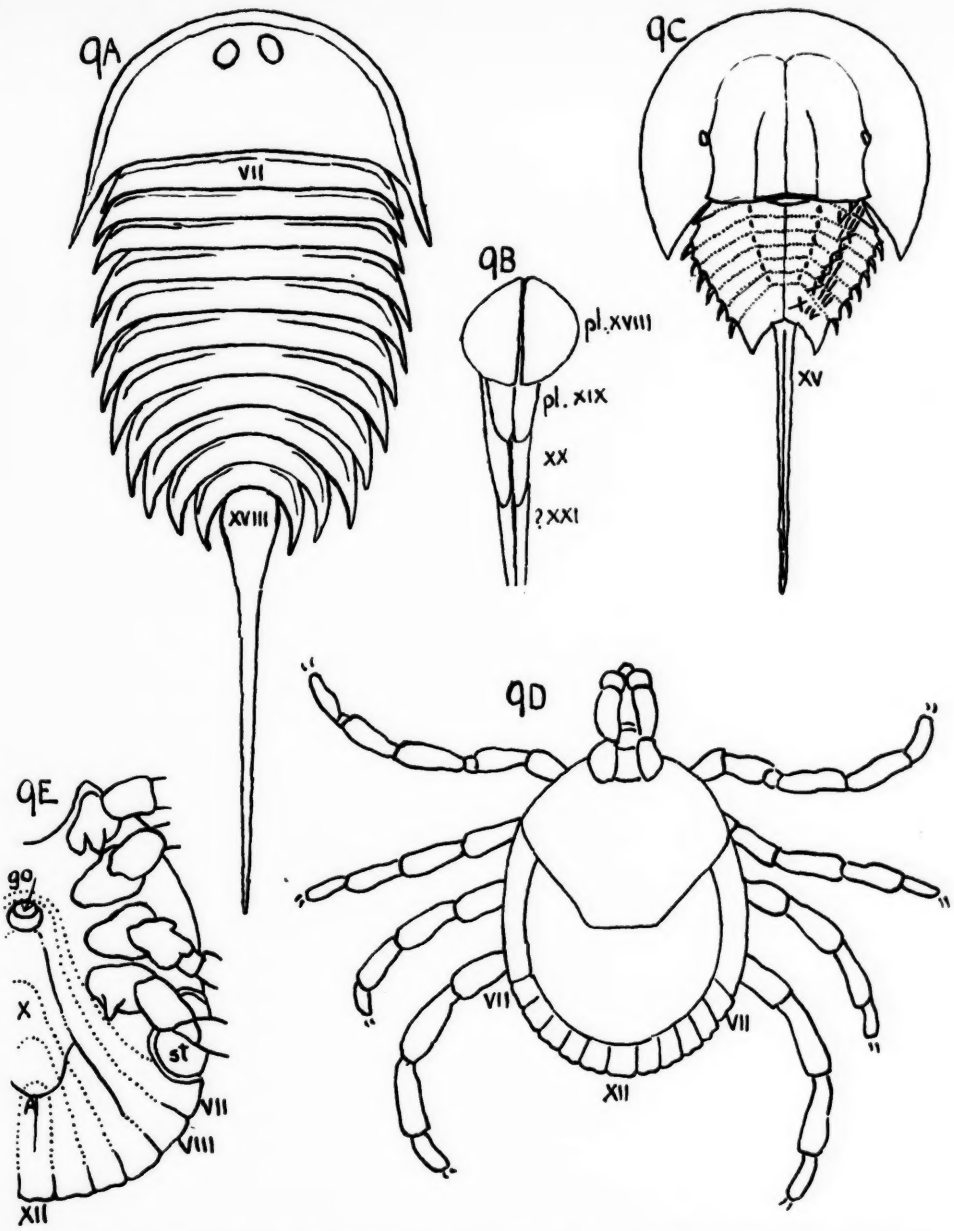
section, but showed that the dorsal plate was missing over the anterior half of each, except for a very narrow doublure in front. He also showed that there were gills above the posterior half of all leaf-feet.

B—Diagram expressing the views of Størmer and Petrunkevitch: the first tergite is the pregenital, VII; the last segment-ring has tergite XVIII, and is followed by a telson; the metastome is the reduced united appendages of segment VII; the "operculum" and the other four leaf-feet are each a pair of coalesced appendages, viz. of segments VIII to XII, and bear gills on the posterior dorsal half.

C—Diagram illustrating the view of Raw. Tergite VII is sunk, reduced, and advanced under the carapace; the first visible tergite is thus genital VIII; and by making the last segment-ring a coalescence of two (XIX and XX) the tail-spine is segment XXI, as in *Olenellus*, in front of which is the *secondary* anus. The metastome is the reduced appendages of VII; each ventral plate behind this is compounded of a sternum followed by a pair of appendages of the next succeeding segment. Thus the last plate is sternum XII and the appendages of XIII (which, reduced to a segment length, is the case in the scorpion). The so-called "operculum" has, however, besides sternum VIII and appendages IX, a reduced sternum VII and the endopodite of the genital VIII coalesced with it.

D—New interpretation of the "operculum" of *Eurypterus*. The type figured marks the sex which Holm regarded as the male, but which now Størmer and others regard as the female. The normal scale-markings which are spread extensively over it are omitted: only the stronger ones which divide it into three strips being represented. The middle strip is sternum VIII and between its two halves is the residue of VIII's appendages labelled "En.Ap. VIII". In front of VIII is sternum VII and behind it the gill-bearing appendage of IX regarded as modified "exopodite," Ap. Ex. IX.

E—Longitudinal diagram section of the scorpion showing the abdominal segmentation and the lung-books of segments X to XIII as sessile appendages, each representing the gill-branch of the biramous appendages of the ancestral trilobite, but transformed into the ventral body wall (modified after Newport & Blanchard in Parker & Haswell, 1949).



TEXT-FIG. *9*—Diagrams illustrating chelicerates with 12, with 9 and with 6 significant abdominal segments.

A—Outline restoration of *Aglaspis spinifer* Raasch. Its semi-ovoid body is represented as found, flattened by sedimentation, but the tail-spine as in life, cylindro-conic, though in the fossils it is collapsed and widened (based on Raasch, 1939, pls. 1,7).

B—Ventral aspect of the tail-spine of an aglaspid *U-arthrus instabilis* Raasch. It is flattened and is interpreted here as being underlain by the pleura of its segment, which wrap round it so that their anterior edges meet in the mid-ventral line constituting the post-ventral plate of Raasch. These again are followed by the subverted pleura of reduced segments XIX, XX and perhaps XXI. (after Raasch, 1939, pl. 13, fig. 3).

C—Dorsal aspect of a king crab with the abdominal segmentation indicated and numbered. It embraces three triadic merocycles instead of five as in *Olenellus*. The anterior segment VII has its median part reduced and withdrawn under the prosoma in agreement with the forward advance of chilaria (largely after Petrunkevitch, 1947C).

D,E—Two ticks. *D*, Dorsum of the tick *Amblyomma paulopunctatum*. *E*, Ventrum of *Amblyomma coelebs* without the capitulum. Both are females. The external boundaries of the abdominal segments are indicated by numbers, and in *E* a ventral distribution of them is suggested by dotted lines (Both copied from Robinson, 1926). st = left respiratory stigma, A = anus, G.O. = genital aperture.

REFERENCES

ANDRÉ, MARC, 1949, Acari, *in* Grassé, Traité de Zoologie: vol. 7, p. 794.

BÖRNER, C., 1901, Zur äusseren Morphologie von Koenenia mirabilis Grassé: Zool. Anz., vol. 24, p. 537.

——, 1921, Die Gliedmassen der Arthropoden, *in* A. Lang, Handbuch der Morphologie der wirbellosen Tiere.

BORRADAILE, L. A., POTTS, F. A., EASTHAM, L. E. S., & SAUNDERS, J. T., 1935, 1941, The Invertebrata: Cambridge Univ. Press.

BRAUER, A., 1894–5, Beiträge zur Kenntnis der Entwicklungsgeschichte der Scorpions: Zeitschr. wiss. Zoologie, vol. 57, 59.

BRISTOWE, W. A., & MILLOT, J., 1932, The liphistiid spiders: Zool. Soc. London, Proc., p. 1015.

BURLING, L. D., 1916, *Paedumias* and the Mesonacidae: Ottawa Naturalist, vol. 30.

BUXTON, B. H., 1917, Notes on the anatomy of arachnids: Jour. Morph. 1917.

CLARKE, J. M., 1901, *Pseudoniscus* in the *Eurypterus* beds of New York: Rep. New York State Paleont. for 1900, 54th Ann. Rep.

——, & RUEDEMANN, R., 1912, The Eurypterida of New York: New York State Mus. Mem. 14.

DEMOLL, R., 1914, Die Augen von *Limulus:* Zool. Jahrb. Abt. Anat. 38.

DOUGLAS, J. R., 1943, The internal anatomy of *Dermacentor andersoni* Stiles: Univ. California Pubs. Ent.

DUNBAR, C. O., 1923, Kansas Permian insects, Pt. 2. *Palaeolimulus*, a new genus of Paleozoic Xiphosura . . . : Am. Jour. Sci., ser. 5, vol. 5, p. 443.

——, 1925, Antennae in *Olenellus getzi*, n. sp.: Am. Jour. Sci., ser. 5, vol. 9, p. 303.

FEDOTOV, D., 1924, On the relations between the Crustacea, Trilobita, Merostomata and Arachnida: Bull. Acad. Sci. Russie, p. 383.

FAGE, L., 1949, Mérostomacés, *in* Grassé, Traité de Zoologie: vol. 6, p. 219.

GERHARDT, U., 1935, Chelicerata, Merostomata, Xiphorura; *in* Kükenthal-Krumbach, Handbuch der Zool., Bd. 3, Abt. 2.

HANDLIRSCH, A., 1926–7, Arthropoda, Einleitung: *in* Kükenthal-Krumbach, Handbuch der Zool., Bd. 3.

HANSEN, H. J., 1930, Studies on Arthropoda. III. On the comparative morphology of the appendages in the Arthropoda . . . Arachnida: Copenhagen.

——, & SORENSEN, W., 1904, On two orders of Arachnida: Opiliones, esp. the s.o. Cyphophthalmi and Ricinulei, the fam. Cryptostemmatoidae: Cambridge Univ. Press.

HANSTRÖM, B., 1926, Das Nervensystem und die Sinnesorgane von *Limulus polyphemus:* Lunds Univ. Arskr., vol. 22.

——, 1928, Vergleichende Anatomie des Nervensystems der wirbellosen Tiere: Berlin.

HEDGPETH, J. W., 1947, On the evolutionary significance of the Pycnogonida: Smithsonian Misc. Coll., vol. 106, no. 18.

HELFER, H., & SCHLOTTKE, E., 1935, Pantopoda, *in* Bronn, Klassen und Ordnungen des Tierreichs 5, 4, 2, 1 and 2.

HENRY, L. M., 1950, The cephalic nervous system of Limulus polyphemus Linnaeus etc. Microentomology, vol. 15, part 4, p. 129.

HIRST, S., 1923, On some Arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Averdeensh.). Ann. Mag. Nat. Hist. 9, 12.

HOLM, G., 1898, Über die Organisation von *Eurypterus fischeri* Eichw: Acad. Imp. Sci., St. Petersburg, Mém., ser. 8, vol. 8, no. 2.

IWANOV, P. P., 1933, Die embryonale Entwicklung von *Limulus molluccanus:* Zool. Jahrb., Abt. Anat., vol. 56.

KÄSTNER, ALFRED, 1932–7, Arachnida, *in* Kükenthal-Krumbach. Handbuch der Zool.

——, 1940, Scorpions, *in* Kükenthal-Krumbach, Handbuch der Zool., vol. 3, Hälfte 2.

KIAER, J., 1916, The Lower Cambrian *Holmia* fauna at Tømten in Norway: Vidensk selsk. Skrift, 1, no. 10.

KINGSLEY, J. S., 1892–3, The embryology of *Limulus:* Jour. Morph., vol. 7, 8.

KISHINONYE, K., 1892, Development of *Limulus longispina:* Jour. Sci. Coll. Japan, vol. 5.

LANKESTER, E. R., 1881, *Limulus*, an Arachnid: Quart. Jour. Micros. Sci., vol. 21.

——, 1910–11, Arachnida, Encycl. Britannica, 11th ed.

——, & BOURNE, A. G., 1883, The minute structure of the lateral and central eyes of *Scorpio* and *Limulus:* Quart. Jour. Micros. Sci., vol. 23, p. 177.

——, BENHAM, W. B. S., & BECK, E. J., 1885, On the muscular and endoskeletal systems of *Limulus* and *Scorpio* . . . : Zool. Soc. London, Trans., vol. 11, p. 311.

LAURIE, M., 1893, The anatomy and relations of the Eurypteridae: Roy. Soc. Edinburgh, Trans., vol. 37, no. 2, p. 24.

MILLOT, J., 1949, Morphologie externe des Arachnides, *in* Grassé, Traité de Zoologie, vol. 6, p. 263.

——, 1949, Five arachnid orders, ibid., p. 520–760.

——, & VACHON, M., 1949, Scorpions, ibid., p. 386.

MILNE-EDWARDS, A., 1872–3, Récherches sur l'anatomie des Limules: Ann. Sci. Nat., vol. 17.

MOORE, P. F., 1941, On gill-like structures in the Eurypterida: Geol. Mag., vol. 78, p. 62.

NIEZKOWSKI, J., 1859, Der Eurypterus remipes von der Insel Oesel: Arach. Naturgesch. Liv. Esth. und Kurlands, 1, vol. 2.

NUTTALL, G. H. F., WARBURTON, C., COOPER, W. F., & ROBINSON, L. E., 1908, 1911, 1915, 1926, Ticks, a Monograph of the Ixodoidea: Cambridge Univ. Press.

O'CONNELL, M., 1916, The habitat of the Eurypterida: Buffalo Soc. Nat. Sci. Bull., vol. 11, no. 3.

OWEN, R., 1872–3, Anatomy of the king crab: Linn. Soc. London, Trans., vol. 28.

PARKER, G. H., 1887, Eyes of scorpions: Mus. Comp. Zool., Harvard, Bull., vol. 13, p. 173.

PATTEN, W., 1896, Variations in the development of *Limulus polyphemus:* Jour. Morph., vol. 12.

——, & REDENBAUGH, W., 1899, Studies on *Limulus:* Jour. Morph., vol. 16.
PETRUNKEVITCH, A., 1913, Terrestrial Paleozoic Arachnida of North America: Conn. Acad. Arts Sci., Trans., vol. 18.
——, 1922, The circulatory system and segmentation in Arachnida: Jour. Morph., vol. 36, p. 157.
——, 1934, New observations on moulting and mating in Tarantulae: New York Entom. Soc., Jour., vol. 42, p. 289.
——, 1945, Palaeozoic Arachnida of Illinois: Ill. Sci. Papers, vol. 3, no. 2.
——, 1947a, Scorpions: Encycl. Britannica.
——, 1947b, Spiders: Encycl. Britannica.
——, 1947c, Xiphosura: Encycl. Britannica.
——, 1948a, Arachnida: Encycl. Britannica.
——, 1948b, Eurypterida: Encycl. Britannica.
——, 1949, A study of Palaeozoic Arachnida: Conn. Acad. Arts Sci., Trans., vol. 37.
POCOCK, R. I., 1901, The Scottish Silurian scorpion: Quart. Jour. Micros. Sci., vol. 44, p. 291.
——, 1911, Terrestrial Carboniferous Arachnida of Great Britain: Palaeont. Soc., 1910.
RAASCH, G. O., 1939, Cambrian Merostomata: Geol. Soc. Am., Spec. Pap. 19.
RAW, F, 1924, The development of *Leptoplastus salteri* Callaway and other trilobites . . . : Geol. Soc. London, Abs. Proc., no. 1122.
——, 1925, The development of *Leptoplastus salteri* Callaway and other trilobites. (Olenidae, Ptychoparidae, Conocoryphidae, Paradoxidae, Phacopidae and Mesonacidae): Geol. Soc. London, Quart. Jour., vol. 81, p. 223.
——, 1927, The ontogenies of trilobites and their significance: Am. Jour. Sci., ser. 5, vol. 14, p. 7, 131 and 240.
——, 1936, The Mesonacidae of Comley in Shropshire, with a discussion of classification within the family: Geol. Soc. London, Quart. Jour., vol. 92, p. 236.
——, 1937, Systematic position of the Olenellidae (Mesonacidae): Jour. Paleont., vol. 11, p. 575.
——, 1949, Some stages in the evolution of the nervous system and the fore-gut of the polychaet: Smithsonian Misc. Coll., vol. 11, no. 8.
——, 1952, A note on Ross' "Ontogenies of three Garden City trilobites": Jour. Paleont., vol. 25, p. 854.
——, 1953, The external morphology of the trilobite: Jour. Paleont., vol. 27, p. 82.
——, 1955, The Malacostraca: their origin, relationships and phylogeny: Mag. Nat. Hist., ser. 12, vol. 8, p. 731.
RAYMOND, P. E., 1920, The appendages, anatomy and relationships of trilobites: Conn. Acad. Arts and Sci., Mem. 7.
——, 1944, Late Palaeozoic Xiphosurans: Mus. Comp. Zool., Harvard, Bull., vol. 94, p. 473.
RESSER, C. E., 1931, A new Middle Cambrian merostome crustacean: U. S. Nat. Mus., Proc., vol. 79.
——, & HOWELL, B. F., 1938, Lower Cambrian *Olenellus* zone of the Appalachians: Geol. Soc. Am., Bull., vol. 49.
RICHTER, R., & E., 1929, *Weinbergina opitzi* n.g., n. sp. ein Schwerträger (Merost. Xiphos.) aus den Devon Rheinland: Senkenbergiana, vol. 11.
ROBINSON, L. E., 1926, The genus *Amblyomma:* Cambridge Univ. Press (or see Nuttall, G. H. F.)
RUEDEMANN, R., 1916, The presence of a median eye in trilobites: New York State Mus., Bull. 189.
——, 1925, Recent publications on the origin and habitat of the Eurypterida: Am. Jour. Sci., ser. 5, vol. 7, p. 227.
ROEWER, C. F., 1932–4, Solifugae Palpigradi, *in* Bronn, Klassen und Ordnungen, p. 1–723.
——, 1936–40, Chelonethi: ibid, p. 1–354.
SCHMIDT, F., 1883, Die Crustaceen Fauna der Eurypterus Schichten von Rootziküll auf Oesel: Acad. Imp. Sci., St. Petersburg, Mem.
SCHEURING, L., 1913, 1914, Die Augen der Arachnoideen I & II: Zool. Jahrb. Abt. Anat. Ont., vol. 33, 37.
SCHULTZE, P., 1936, Trilobita, Xiphosura, Acarina: eine morphologische Untersuchungen . . . : Zeitschr. Morph. Ökol. Tiere, Bd. 32, Abt. 2.
SCHUSTER, C. N., 1953, Odyssey of the horse-shoe crab: Audubon Magazine, vol. 55, no. 4, p. 162.
SNODGRASS, R. E., 1948, The feeding organs of Arachnida including mites and ticks: Smithsonian Misc. Coll., no. 3944.
——, 1952, A textbook of arthropod anatomy: Cornell Univ. Press.
STØRMER, L., 1933, Are the trilobites related to the Arachnida?: Am. Jour. Sci., vol. 26.
——, 1933, Merostomata from the Downtonian Sandstone of Ringerike, Norway: Skr. Vid. Akad. Oslo I. M.-N. Kl., 1933, no. 10.
——, 1934, Downtonian Merostomata from Spitzbergen, with remarks on the sub-order Synziphosura: ibid., 1934, no. 3.
——, 1941, Studies on trilobite morphology. II. The larval development, the segmentation and the sutures, and their bearing on trilobite classification: Norsk geol. tidsskr., vol. 21.
——, 1944, On the relationships and phylogeny of fossil and Recent Arachnomorpha . . . : Skr. Vid.-Akad. Oslo, I. M.-N. Kl., 1944, no. 5.
——, 1949, Trilobitomorphs, *in* Grassé, Traité de Zoologie, vol. 6, p. 161.
——, 1951, Studies on trilobite morphology. III. The ventral cephalic structures with remarks on the zoological position of the trilobites: Norsk geol. tidsskr., vol. 29, p. 108–158.
——, 1952, Phylogeny and taxonomy of fossil horseshoe crabs: Jour. Paleont., vol. 26, p. 630.
STROMER VON REICHENBACH, E., 1907, Über Molukkenkrebse: Zeitschr. deutsch. geol. Gesell., Monatsber.
TATTERSALL, W. M., & O. S., 1951, The British Mysidacea: The Ray Society, no. 136.
THORELL, T., 1886, On *Proscorpius osborni* Whitf.: Am. Nat., vol. 20.
——, & LINDSTRÖM, G., 1885, On a Silurian scorpion from Gotland: Kongl. Svenska Vetensk. Akad. Handl., vol. 21, no. 9.
VACHON, MAX., 1949, Pseudoscorpiones, *in* Grassé, Traité de Zoologie, vol. 6, p. 437.

VANDEL, A., 1949, Généralités sur les Arthropodes, *in* Grassé, Traité de Zoologie, vol. 6.
VERSLUYS, J., & DEMOLL, R., 1922, Das Limulus Problem . . . : Ergebn. y. Fortschr. d. Zool., vol. 5.
VITZTHUM, H. G., 1931, Acari = Milben, *in* Kükenthal-Krumbach, Handbuch der Zool.
——, 1940–43, Acarina, *in* Bronn, Klassen und Ordnungen des Tierreichs, vol. 5, p. 1–1011.
WALCOTT, C. D., 1910, *Olenellus* and other genera of the Mesonacidae. Smithsonian Misc. Coll., vol. 53, no. 6.
——, 1921, Notes on the structure of *Neolenus:* ibid., vol. 67, no. 7.
WESTERGÅRD, A. H., 1936, *Paradoxides oelandicus* beds of Öland. Sveriges geol. Undersök., ser. C, no. 394.
WHITFIELD, R. P., 1885, On a fossil scorpion from the Silurian rocks of America: Am. Mus. Nat. Hist. Bull., vol. 9.
WILLS, L. J., 1925, The morphology of the Carboniferous scorpion *Eobuthus* Fritsch: Linn. Soc. Zool. Jour., vol. 36, p. 87.
——, 1934, Notes on a rare Carboniferous scorpion from the Oranje Nassau Mine: Jaarverslag Geol. Bur. Heerlen, no. 3.
——, 1947, A Monograph of the British Triassic scorpions: Palaeont. Soc.
WITH, C. J., 1904, The Notostigmata, a new suborder of Acari., Videnskab. Medd. Naturhist. Foren. Kjobenhavn, vol. 25, p. 137.
WOODWARD, H., 1866–78, A Monograph of the British fossil Crustacea of the Order Merostomata: Palaeont. Soc.

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QUANTITATIVE TRILOBITE STUDIES II. MEASUREMENT OF THE DORSAL SHELL OF NON-AGNOSTIDEAN TRILOBITES

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ABSTRACT—A set of standard names and symbols for various precisely defined dimensions of the trilobite dorsal shield is proposed together with a list of minimum essential measurements needed to describe the non-agnostidean trilobite cephalon in quantitative terms.

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THIS article, like the first in this series, was submitted to a number of colleagues for their comments. W. C. Bell, W. R. Evitt, and B. F. Howell all made suggestions. Christina Lochman revised the original terminology at length to correspond with that to be used in the section on trilobites in the Treatise on Invertebrate Paleontology.

INTRODUCTION

One of the most pressing problems that faces the student of quantitative trilobite morphology is the precise definition of the units measured. There are, for instance, at least 3 ways to represent glabellar length and at least 8 for head length. Not all are equally useful or "natural," but they exist and must be precisely delineated so that subsequent students will be able to repeat exactly the original measurements. This, of course, means that an elaborate terminology is inescapable—a terminology more complex than any now in use, although it should necessarily be based on current qualitative, descriptive nomenclature. It also seems that a sketch showing the measurements used might well be included in each paper to clarify the written description of the measurement (see Frederickson, 1949, p. 342; Shaw, 1950, p. 588, fig. 4; 1952, p. 462, fig. 2).

In the pages that follow an attempt is made to develop a consistent and reasonably compact set of terms for the measurable units. There will undoubtedly be some objection to the erection of such a set of names, but it is done only after long reflection and in the conviction that without precise terms for our units we cannot achieve precision in our quantitative discussions.

The mechanics of measurement.—All of the species studied quantitatively in the preparation of this and the preceding paper have been sufficiently small so that the great majority of specimens could be measured by means of a micrometer eyepiece set in a binocular microscope. This permits measurements to 0.01 mm. where needed. Large trilobites can be measured with adequate accuracy by means of calipers, for there is no reason to measure parts to 0.01 mm. on animals 300 mm. or longer.

It is important that care be taken to note where preservation has affected the size of measurements. For example, the length of the head of a trilobite with a thick test may be appreciably longer than the length of the exfoliated internal mold of the same species. One important reason for the emphasis laid in this paper on measuring furrows from their deepest point is that this procedure minimizes the effect of exfoliation.

It is basic to any system of measurement that a standard orientation of the trilobite be used. Two approaches can be used: (1) Take all measurements normal to the surface (or the chord of a convex feature) being measured, or (2) orient the trilobite one way for all measures. The first method has the advantage of giving true size on sloping parts, but it has the serious disadvantage of requiring repeated manipulation of the specimen. The second method requires only one orientation of the specimen and has the very real advantage of giving measurements that can be compared with those taken from photographs. Also, measurements from a single orientation more closely approximate the visual impression of the specimen. The single-orientation

method is used throughout this article with one exception, which is noted explicitly.

If a single orientation is used, it is necessary to choose some reference plane, so that the orientation used is constant. In all examples studied to date it has been fully satisfactory to place the palpebral lobe (or its chord, where the lobe is curved) horizontal. An essentially similar orientation may be obtained by orienting the dorsal furrows opposite the middle of the glabella horizontally; this is useful in eyeless forms. Obviously, there are exceptions to both of these methods, but the horizontal palpebral lobe will serve adequately for the great majority of trilobites, and its use is assumed in all that follows, except where specifically noted to the contrary.

Thoracic segments offer little problem in orientation. They may be oriented with the dorsal furrow (or its chord, where the furrow is convex) horizontal.

The pygidium is most consistently measurable by placing horizontal the plane determined by the ventral margin of the border, where the border rolls under to form the doublure.

MEASUREMENTS

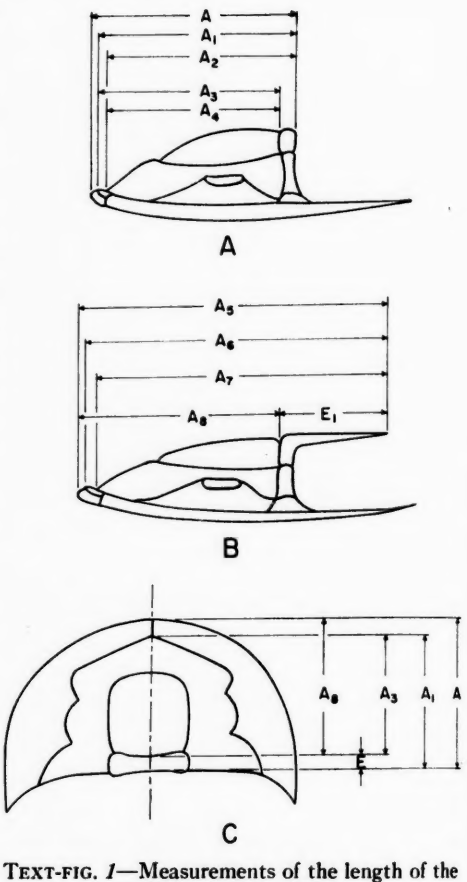
Measurements of Length on the Cephalon or Cranidium

The first measurement that normally presents itself to the investigator is that of the length of the head. Depending upon the specimen and its preservation, eight measurements may be applicable (Fig. 1). All head lengths may be designated by the letter A.*

Total cephalic length (A) measured from the rear edge of the occipital ring to the front, center edge of cephalon. This is the most natural unit if the entire cephalon is present, but since complete specimens are uncommon this unit is not often of practical use. More useful is the:

Total cranidial length (A_1) measured from the rear of the occipital ring to the front edge of the cranidium in the sagittal plane.

* In all measurements I have chosen what seems to me to be the most natural unit to be designated by a single letter. The more artificial or less commonly useful units are designated by subscript numerals in their approximate order of importance.



TEXT-FIG. 1—Measurements of the length of the cephalon and cranidium.

This unit is more useful than the total cephalic length (although in some cases it is not measurably different from it) because it permits subsequent comparison of fragmented cranidia with the original complete cephala and should be given wherever possible in addition to the total cephalic length (A). In addition the:

Occipital intramarginal cephalic length (A_2) measured from the rear of the occipital ring to the deepest point in the marginal furrow in the sagittal plane should be given to permit adequate comparison with specimens for which the anterior border was not fully recovered, making the total cranidial length (A_1) unobtainable. This is the most constantly useful standard as a measure of "growth stage," for its use permits the inclusion of many specimens that would not

otherwise be available if the total cranidial length (A_1) were insisted upon.

Pre-occipital cranidial length (A_3) is measured from the front of the cranidium to the deepest point in the occipital furrow, in the sagittal plane. This unit, like the next, is useful if specimens are commonly found with the occipital ring damaged. It is not a natural unit.

Pre-occipital intramarginal cranidial length (A_4) is measured from the deepest point in the occipital ring to the deepest point in the marginal furrow, in the sagittal plane. It is useful in cases where both the anterior cranidial margin and the occipital ring are commonly damaged.

Three measurements are possible on specimens retaining an occipital spine (Text-fig. 1B):

Total spinal-cephalic length (A_5) measured from the rear tip of the spine to the front of the cephalon in the sagittal plane. This is a natural unit but one rarely available because of preservation defects.

Total spinal-cranidial length (A_6) measured from the rear tip of the spine to the front edge of the cranidium, in the sagittal plane.

Intramarginal-spinal crandial length (A_7) measured from the rear tip of the occipital spine to the deepest point in the marginal furrow, in the sagittal plane.

Pre-occipital cephalic length (A_8) measured from the deepest point in the occipital furrow to the front edge of the cephalon. This measurement is a possible unit, but an unlikely one, for if the cephalon were preserved intact the natural unit would be the total cephalic length (A). The only case in which this unit might be used would be in conjunction with a measurement of the occipital ring (E) or occipital spine (E_1) as shown in Text-fig. 1B and 1C. The measurement of the occipital ring and spine is described below.

Certain other special measurements might be made on the cephalon, particularly in exsagittal planes, but these are deemed too specialized to warrant precise definition at this time. It is also possible to measure radii from established points on the cephalon to various points on the margin of the cephalon to represent curvature of the cephalic margin, but these are also subject to modification by circumstances of preservation, the precise argument to be demonstrated, etc., so that no specific suggestions are made here for their definition.

Measurements of glabellar length.—The discussion of what constitutes the glabella in a trilobite is not particularly germane to the problem at hand, but it is best to state clearly that in this paper the term *glabella* excludes the occipital ring.

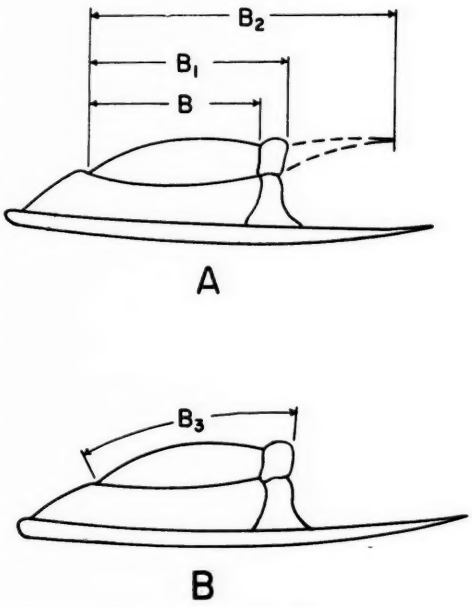
There are three simple measurements on the glabella (Text-fig. 2).

Total glabellar length (B) measured from the deepest point in the occipital ring to the deepest point in the dorsal furrow, in the sagittal plane.

Occipital glabellar length (B_1) measured from the rear of the occipital ring to the deepest part of the dorsal furrow, in the sagittal plane.

Total glabellar-spinal length (B_2) measured from the rear tip of the occipital spine to the deepest part of the dorsal furrow, in the sagittal plane.

Length of the glabellar contour (B_3). Gaines (1951, pp. 608–609) has used an elaborate method for measuring glabellar length involving the projection of the lateral view of the glabella on a ground glass at a



TEXT-FIG. 2—Measurements of glabellar length.

fixed magnification, fitting a wire to the glabellar contour, measuring the length of the straightened wire, and reducing the length by the factor of magnification. This method was useful in a study of the tumid glabella of *Irvingella* such as Gaines made, but it does seem that it should necessarily become a standard type of glabellar measurement. The principal objections are (1) the elaborateness of the technique, which is impossible to duplicate without similar camera equipment, and (2) the fact that for most trilobites, including those with inflated glabellae, the measurements B, B_1, and B_2 seem to be adequately descriptive although far less complicated.

Measurement of the length of palpebral lobes.—Palpebral lobes do not now play a large part in the discrimination of species, so that measurements of their length seem to be at best purely descriptive. There seem to be two groups of palpebral lobes; those which are essentially symmetrical, with their front and rear ends nearly aligned (Text-fig. 3A, D), and those that are asymmetric, with the front end closer to the midline of the cephalon than the rear (Text-fig. 3B,C). Three types of measure suggest themselves:

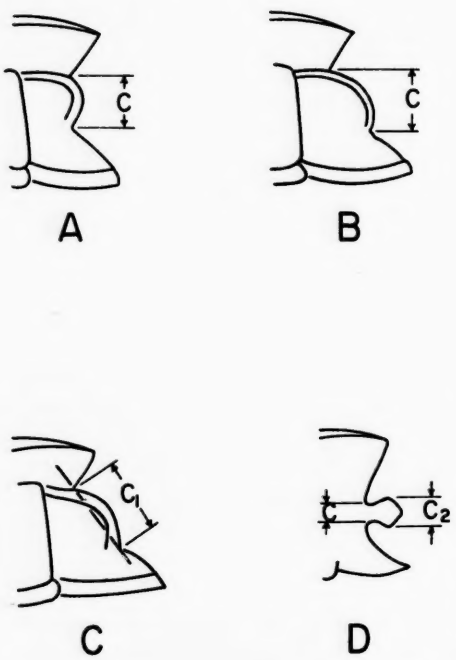
Exsagittal palpebral length (C) measured between the ends of the palpebral lobes as projected into an exsagittal plane lying parallel to the sagittal plane. This measure has the advantage of not requiring reorientation of the specimen and is the logical one to make on symmetrical palpebral lobes (Text-fig. 3A); it can be used on the asymetrical types (Text-fig. 3B), but here it has the disadvantage of measuring only the projection of the palpebral length and may thereby give a false impression of the true length. In the asymmetric lobes we may substitute the:

Palpebral chord length (C_1) measured directly from one end of the lobe to another without regard for the direction (Text-fig. 3C).

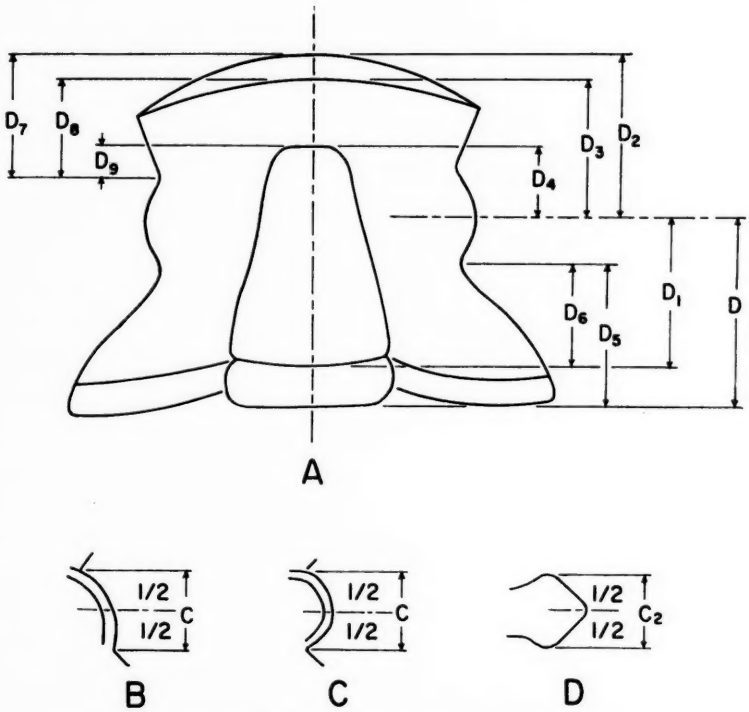
Maximum palpebral length (C_2) is a useful dimension in those rare forms whose palpebral lobes are flaplike and are longest at some distance from their point of attachment to the rest of the cranidium (Text-fig. 3D). In such cases the maximum length is generally easier to determine than the exsagittal length (C) because it is often difficult to expose completely the points of juncture between the lobes and cranidium.

Position of the eyes.—This measure is one of fundamental importance. It seems to be of generic significance (Lochman, 1947, p. 60; Shaw, 1952, p. 465, text-fig. 3E). The variety of ways of locating the eye is great, but inasmuch as the palpebral lobes are a cranidial feature I believe it is more natural to use points on the cranidium to locate the lobes than points outside the facial sutures; only this sort of measurement is indicated in Text-fig. 4.

Occipital mid-palpebral distance (D) measured from the mid-point of the rear edge of the occipital lobe to the mid-point of the projection of the lobe into the sagittal plane. This is the most useful of the means of positioning the eye that I have used. By graphing it against the total cephalic length (A) or the total cranidial length (A_1) or the post-occipital intramarginal cephalic length (A_2) we may derive an accurate measure of the eye position in relation to the whole



TEXT-FIG. 3—Measurements of the length of the palpebral lobe.



TEXT-FIG. 4—Measurements of eye position. Sketches B, C, and D show how the midpoint of the palpebral lobe is defined.

head. By comparing this distance (D) with the occipital glabellar length (B_1) we have a measure of the relation of the eye to the glabella.

Pre-occipital mid-palpebral distance (D_1) measured from the mid-point of the projection of the eye into the sagittal plane to the deepest point in the occipital furrow, in the sagittal plane. This is the best measure of eye position where there is an occipital spine present and should be compared with pre-occipital head lengths A_3, A_4, or A_8. This unit (D_1) should not be compared with head lengths measured from the *rear* of the occipital ring, for the comparison is meaningless. Comparison with the glabella should likewise be with the total glabellar length (B).

Anterior cranidial mid-palpebral distance (D_2) measured from the anterior edge of the cranidium in the sagittal plane to the projection of the mid-point of the palpebral lobe into the sagittal plane. I have not used this measurement, but it could be of great use in the study of the rearward migration of the palpebral lobes during early ontogeny. However, if the post-occipital mid-palpebral distance (D) and the total cranidial length (A_1) are given the anterior cranidial mid-palpebral distance (D_2) can be obtained by subtraction for: $D_2 = A_1 - D$.

Intramarginal mid-palpebral distance (D_3) measured from the deepest point in the marginal furrow in the sagittal plane to the projection of the mid-point of the palpebral lobe into the sagittal plane. This is a useful substitute for the anterior cranidial mid-palpebral distance (D_2) in those cases where the anterior cranidial margin is not commonly preserved.

Anterior glabellar mid-palpebral distance (D_4) measured from the deepest point of the dorsal furrow in front of the glabella, in the sagittal plane, to the mid-point of the palpebral lobe projected into the sagittal plane. This is a valuable measure

of the relation of glabellar length and eye position.

Occipital post-palpebral distance (D_5) measured from the posterior edge of the occipital ring in the sagittal plane to the projection of the rear end of the palpebral lobe into the sagittal plane. This is an "unnatural" unit, but if the outer edges of the palpebral lobes are commonly destroyed, it may be a useful substitute for the post-occipital mid-palpebral distance (D).

Pre-occipital post-palpebral distance (D_6) measured from the deepest part of the occipital furrow in the sagittal plane to the projection of the rear end of the palpebral lobe into the sagittal plane. This rarely useful unit could serve to replace the occipital post-palpebral distance (D_5) in forms bearing an occipital spine.

Pre-cranidial pre-palpebral distance (D_7) measured from the anterior edge of the cranidium in the sagittal plane to the projection into the sagittal plane of the point of intersection of the palpebral lobe and anterior branch of the facial suture. This measure was used by Poulsen (1937, p. 32, 34,35,38).

Intramarginal pre-palpebral distance (D_8) measured from the deepest part of the marginal furrow in the sagittal plane to the projection into the sagittal plane of the point of intersection of the anterior end of the palpebral lobe and the anterior branch of the facial suture. This is a usable substitute for the preceding measurement in cranidia that may have the anterior border destroyed.

Pre-glabellar pre-palpebral distance (D_9) measured from the deepest part of the dorsal furrow in front of the glabella in the sagittal plane, to the projection into the sagittal plane of the point of intersection of the anterior end of the palpebral lobe and the anterior branch of the facial suture. This unit could, in some rare cases, be useful in describing eye position relative to the glabella, but I have not to date ever had occasion to use it.

Sagittal width of the occipital lobe (E) measured from the deepest part of the occipital furrow to the rear edge of the occipital lobe, both in the sagittal plane (Text-fig. 5A).

Length of the occipital spine (E_1) measured from the deepest part of the occipital furrow to the rear tip of the occipital spine, both in the sagittal plane (Text-fig. 5B).

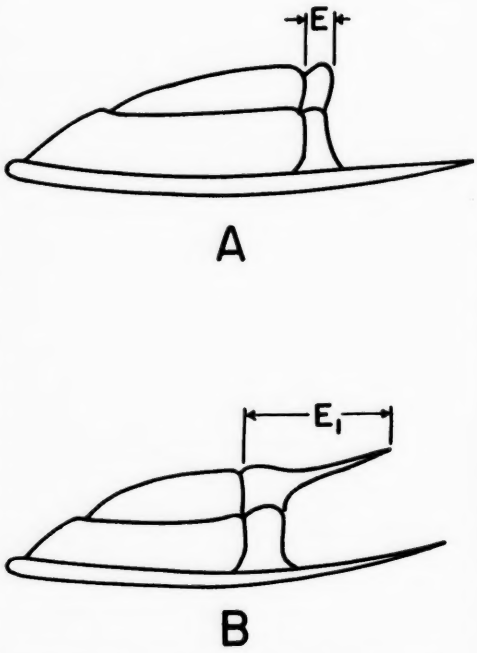
Sagittal width of cephalic frontal area (F) measured from the deepest part of the dorsal furrow to the front edge of the cephalon, both in the sagittal plane (Text-fig. 6).

Sagittal width of cranidial frontal area (F_1) measured from the deepest part of the dorsal furrow to the anterior edge of the cranidium, both in the sagittal plane.

Sagittal width of the anterior border (G) measured from the anterior edge of the cephalon to the deepest part of the marginal furrow, both in the sagittal plane.

In addition, in some specific instances there may be need for various exsagittal widths of the anterior border. Since these would have to be described for each individual case, no attempt is made here to generalize.

Sagittal width of the cranidal border (G_1) measured from the anterior edge of the cranidium to the deepest part of the dorsal furrow, both in sagittal section.



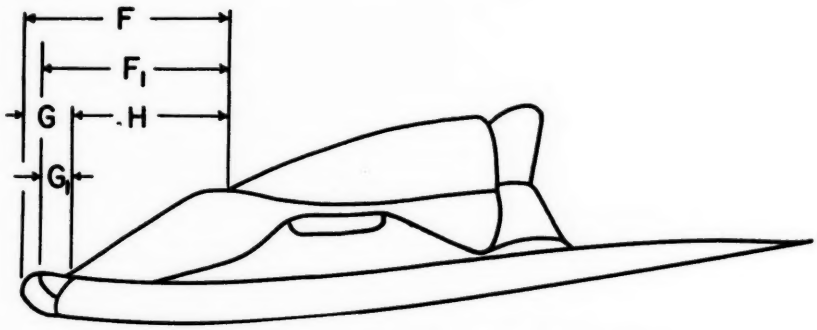
TEXT-FIG. 5—Measurement of the length of the occipital ring and occipital spine.

Sagittal width of the pre-glabeller area (H) measured from the deepest part of the dorsal furrow to the deepest part of the marginal furrow, both in the sagittal plane.

Miscellaneous measurements.—Many other special measurements can be made on trilobite cephala, but all seem to be so special or individualized as not to warrant detailed consideration at this time. The only possible exception to this would be measures of the length of genal spines. To date I have never had a sufficient number of fully preserved specimens of free cheeks to permit quantitative study, so in the absence of actual experience in the matter I refrain from suggesting precise measures.

Another type of measurement for which special techniques would be needed is the length of anterior extensions of the anterior border, as in *Dokimocephalus*, and of the glabella, as in *Ampyx*. The rarity of such structures suggests that measurement of them should be individually tailored, and they, therefore, are not summarized here.

A point of caution may be added here, too. It is possible to make all width measurements on one side of the head and simply double to obtain the whole. This practice is invaluable in measuring damaged specimens, but when entires are available it should not be indulged, for the doubling process applies equally to errors in measurement, and it has been found that frequently such doubled measurements turn out to be erratic in spite of repetition of the measurement and all reasonable checks. Therefore, it has been my practice (Shaw, 1952, p. 465–466, 473, etc.) to indicate such doubled measurements by italicizing them in publication.



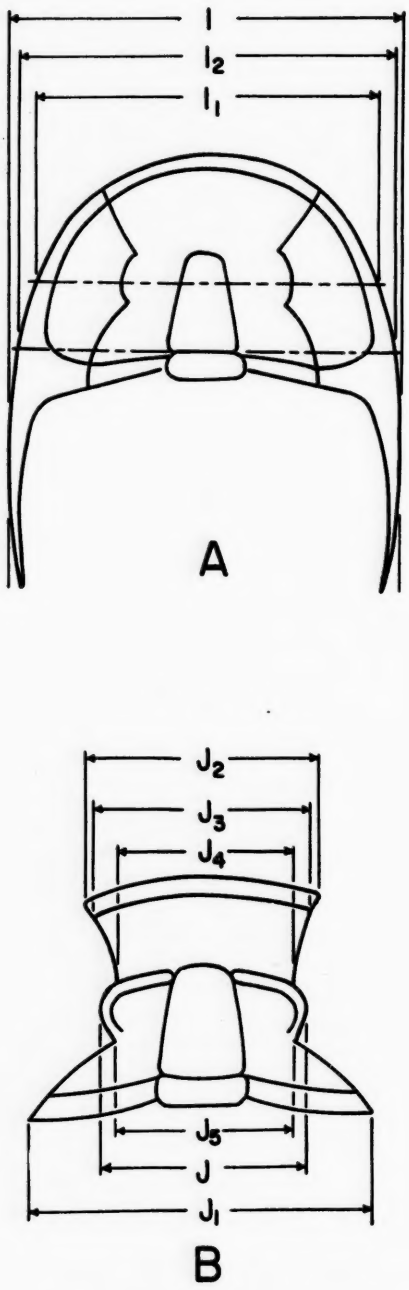
TEXT-FIG. 6—Measurements of length on the frontal area.

Measurements of Width on the Cephalon or Cranidium

Maximum cephalic width (I). The transverse distance between parallel planes tangent to the outermost curves of the edge of the cephalon (Text-fig. 7A). Normally, these points of maximum expansion lie about opposite the occipital ring, but not invariably. This is a "natural" unit to measure, but is not commonly useful because for most species complete cephala are rare; in addition, since the point of maximum spread is not fixed, the measurement may not be comparable from species to species. A far more uniform and useful unit is the:

Palpabral cephalic width (I_1). The transverse distance between outer edges of the cephalon in a vertical plane passing through the mid-points of the palpebral lobes (determined as shown in Text-fig. 4). This is by far the easiest unit to measure for cephalic width.

Occipital cephalic width (I_2) measured between the outer edges of the cephalon in a transverse plane passing vertically through the deepest point of the occipital ring in the sagittal plane. This rather specialized measurement has been used in proparian trilobites, such as *Hardyoides glabrus* (Shaw), 1951, and when compared with the palpebral cranidial width (J) serves as a good measure of the amount of incutting of the facial sutures; it is rather less useful in opisthoparian trilobites.



TEXT-FIG. 7—Measurements of cephalic and cranidial width.

Measurements of cranidial width are shown in Text-fig. 7B. There is little to choose between several of these measurements, so that the order of presentation is not so close an approximation to the order of usefulness as is the case in other units already discussed.

Palpebral cranidial width (J) is the most often available measure in opisthoparian cranidia and is measured normal to two exsagittal planes tangent to the outer extremities of the palpebral lobes. If the palpebral lobes are intact this measurement is extremely easy to make with a moveable micrometer eyepiece, and it is not so subject to perspective distortion as some of the other measurements described below.

Posterior cranidial width (J_1) is measured normal to two exsagittal planes tangent to the outer tips of the posterior limbs. This measure demands perfect preservation of the posterior limbs and uncrushed cranidia, for vertical pressure will widen this dimension noticeably. However, if this unit is available it may be compared with the preceding one to give an estimate of the degree of flare of the posterior branches of the facial sutures.

Maximum width of the frontal area (J_4) is measured normal to two exsagittal planes tangent to the most widely extended points on the frontal area. Normally, these points lie at the anterior end of the facial sutures, where they cut the anterior border, but if the sutures curve inward anteriorly the maximum width will be reached somewhere between the anterior border and the palpebral lobe; in this latter case the use of the maximum width is not recommended, for, like the maximum cephalic width it will not have a constant anterior-posterior position and, thus, may not be comparable between species. The usual case is shown in Text-fig. 7B, and here its use is recommended, providing the tips of the frontal area are not damaged. If these delicate corners are damaged use may be made of the:

Intramarginal width of the frontal area (J_3) measured between the two points where the marginal furrow and the anterior branches of the facial sutures intersect. This is the

most commonly available measure of anterior cranidial width.

Pre-palpebral cranidial width (J_4) and *post-palpebral cranidial width* (J_5) are useful substitutes for the palpebral cranidial width (J) when the outer edges of the palpebral lobes are missing. These two dimensions are measured between the angles generally formed at the intersection of the palpebral lobes with, respectively, the anterior and posterior branches of the facial sutures.

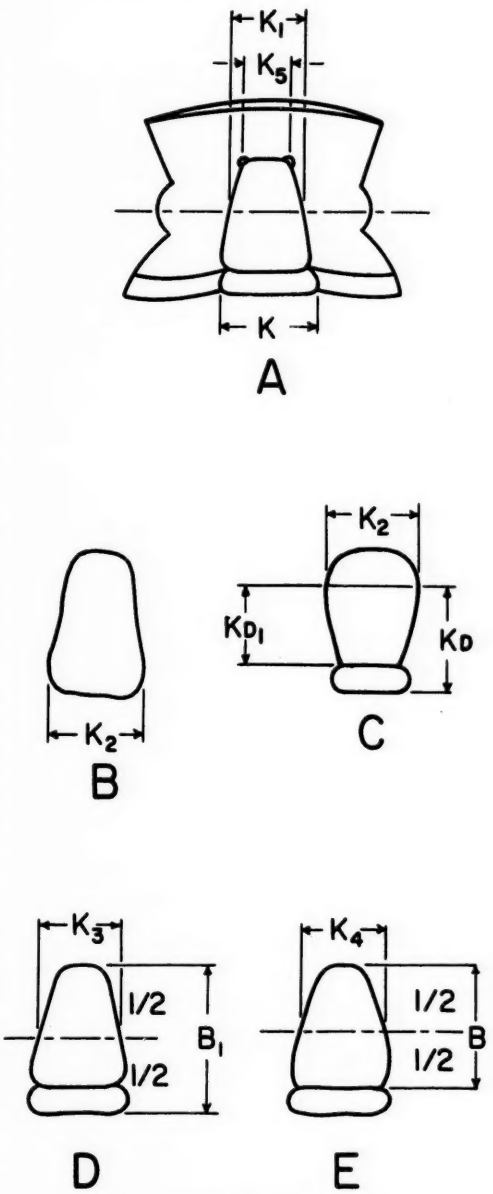
Transverse occipital length (K) is measured from the deepest parts of the dorsal furrow opposite the widest part of the occipital ring. The use of the dorsal furrow eliminates subjective choice of where the occipital ring ends and it permits a measurement fully representative of the part. I have used this as the standard representation of glabellar width in the majority of trilobites studied (Text-fig. 8).

Palpebral glabellar width (K_1) is measured between the deepest parts of the dorsal furrow on opposite sides of the glabella in a vertical plane passing through the mid-points of the palpebral lobes (mid-points determined as in Text-fig. 4). When compared with the occipital width (K) this unit gives a good measure of glabellar taper, and when compared with palpebral cranidial width (J) or palpebral cephalic width (I_1) gives a direct measure of the proportional size of the glabella to the cranidium or cephalon as a whole.

Maximum glabellar width (K_2) is measured normal to two exsagittal planes through the deepest part of the dorsal furrow opposite the widest point of the glabella whether it be anterior or posterior.

This is a useful substitute for the occipital width (K) where there is no occipital ring defined (Text-fig. 8B; and see Shaw, 1950, p. 588, fig. 4, where this dimension is lettered F), or it may be substituted for the palpebral glabellar width (K_1) in corynexochids or other trilobites with anteriorly-expanded glabellae (Text-fig. 8C).

In connection with the latter case it may prove useful in some cases to measure the distance to the point of maximum width (Text-fig. 8C) either from the rear of the occipital ring (Kd) or from the deepest part of the occipital furrow (Kd_1). This is a measure of length, but it was not described



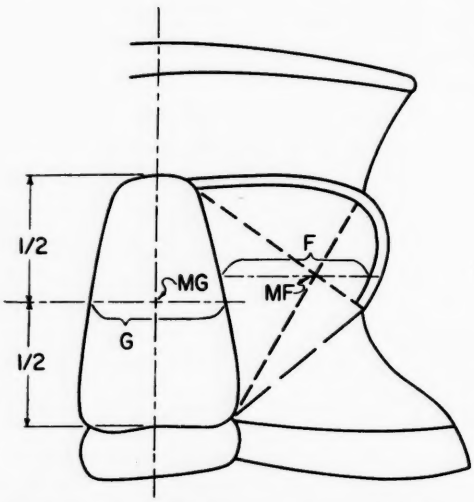
TEXT-FIG. 8—Transverse glabellar and occipital measurements.

earlier because it cannot be separated from the width measurement (K_2).

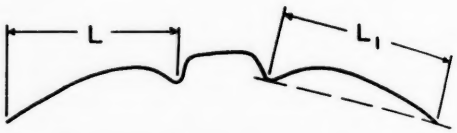
Mid-occipital glabellar width (K_3) is measured between the deepest parts of the dorsal furrow opposite the mid-length of the glabella+occipital ring, as measured in the sagittal plane from the rear edge of the occipital ring to the deepest point in the dorsal furrow. This is far more difficult to measure than the palpebral glabellar width (K_1) and seems to have little practical use.

Mid-glabellar width (K_4) is measured as above, but omitting the occipital ring in the calculation. This is the unit proposed by Lochman (1947, p. 60), who suggested that a ratio be used to compare this width with the width of the fixed cheeks through their mid-points; in practice, the location of the separate mid-points of the glabella and fixed cheeks (particularly the latter) is so complicated (Text-fig. 9) as not to be worth the effort, when more useful statistical results may be obtained by comparing directly the palpebral glabellar width (K_1) and the palpebral cranidial width (J), dimensions that can be obtained in one motion under the microscope.

Anterior glabellar width (K_5) may have occasional use as a substitute for the palpebral glabellar width (K_1). It is measured from one anterior pit to the other. In any species with an anteriorly rounded glabella this dimension would be too poorly defined to be usable.



TEXT-FIG. 9—Ratio between the widths of the glabella and the fixed cheeks as proposed by Lochman (1947, p. 60). MG=midpoint of the glabella. G=width of the glabella at point MG. MF=midpoint of the fixed cheek. F=width of the fixed cheek at point F. F/G=the suggested ratio.



TEXT-FIG. 10—Measurements of the posterior limbs.

Transverse length of posterior limb (L) is the horizontal distance from the deepest part of the dorsal furrow at the rear edge of the cranidium to an exsagittal plane tangent to the outer tip of the posterior limb (Text-fig. 10).

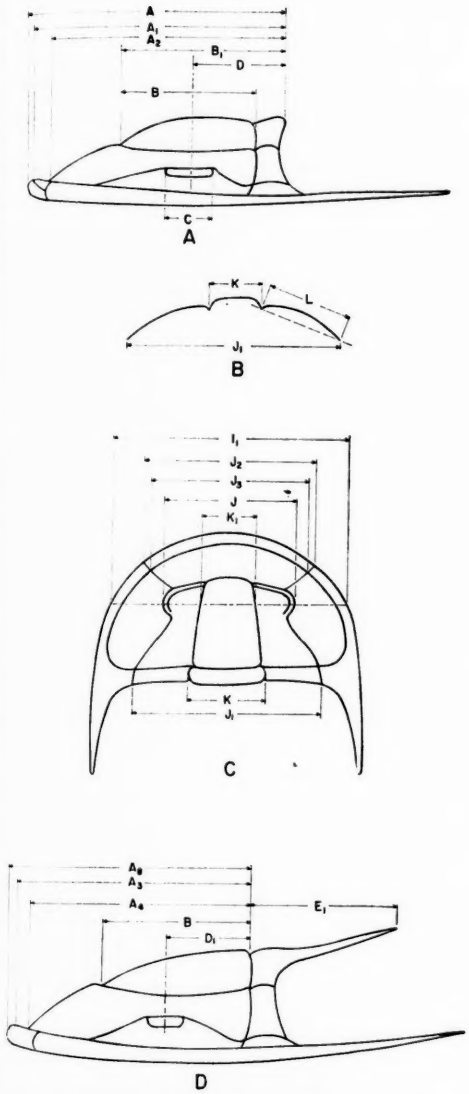
Width of chord of posterior limb (L_1) is the distance from the deepest part of the dorsal furrow at the rear edge of the cranidium measured directly to the tip of the posterior limb. This is a measure of the chord of the arc of the posterior limb. It is recommended over the previous measurement because the convexity of most posterior limbs renders the effect of foreshortening quite severe, and in addition, under the microscope it is not always possible to keep both ends of the limb in focus unless the chord is measured. It is actually easier to measure the posterior cranidial width (J_1) and the occipital width (K) and derive the width of the posterior limb (L) by the formula:

$$L=\frac{J_1-K}{2}$$

Minimum essential measurements.—It is naturally unnecessary to take all of the measurements listed above separately. Text-fig. 11 shows those that seem to be the minimum. From this minimum all other dimensions can be derived by calculation. The minimum list is:

For cephala without occipital spine.

1. Total cephalic length (A).
2. Total cranidial length (A_1).
3. Occipital intramarginal cranidial length (A_2).
4. Total glabellar length (B).
5. Occipital glabellar length (B_1).



TEXT-FIG. *11*—Minimum essential measurements on the non-agnostidean trilobite cephalon.

6. Exsagittal palpebral length (C) or maximum palpebral length (C_2), whichever is applicable. Palpebral chord length (C_1), if desired, must be measured directly.
7. Occipital mid-palpebral distance (D).
8. Palpebral cephalic width (I_1). Maximum cephalic width (I), occipital cephalic width (I_2), and mid-glabellar width (I_3) must be measured directly, if desired, for they cannot be computed.
9. Palpebral cranidial width (J). Note: pre-palpebral cranidial width (J_4) and post-palpebral width (J_5) may be included if it is felt desirable; they cannot be computed.
10. Posterior cranidial width (J_1).
11. Maximum width of frontal area (J_2).
12. Intramarginal width of frontal area (J_3).
13. Transverse occipital length (K).
14. Palpebral glabellar width (K_1). All other suggested measures of glabellar width must be made directly, if desired, for none can be computed. The same applies to the distance to the maximum glabellar width (Kd or Kd_1), although if Kd_1 is available Kd may be computed:

$$Kd = Kd_1 + (B - B_1)$$

15. Width of chord of posterior limb (L_1).

For cephala with occipital spine.

1. Pre-occipital cranidial length (A_3).
2. Pre-occipital intramarginal cranidial length (A_4).
3. Pre-occipital cephalic length (A_8).
4. Total glabellar length (B).
5. Exsagittal palpebral length (C) or maximum palpebral length (C_2), whichever is applicable. Palpebral chord length (C_1), if desired, must be measured directly.
6. Pre-occipital mid-palpebral distance (D_1).
7. Length of the occipital spine (E_1).

8–15. Same 8–15 listed above.

From these minimum measurements all other units not in the list above can be obtained by computation as follows:

$A_5 = A_8 + E_1$

$A_6 = A_3 + E_1$

$A_7 = A_4 + E_1$

$B_2 = B + E_1$

B_3 = not recommended; cannot be computed.

$D_2 = A_1 - D$ or $A_8 - D_1$

$D_3 = A_2 - D$ or $A_4 - D_1$

$D_4 = B_1 - D$ or $B - D$

$D_5 = D - 1/2C$

$D_6 = D - 1/2C - (B_1 - B)$ or $D_1 - 1/2C$

$D_7 = A_1 - D - 1/2C$ or $A_8 - D_1 - 1/2C$

$D_8 = A_2 - D - 1/2C$ or $A_4 - D_1 - 1/2C$

$D_9 = B_1 - D - 1/2C$ or $B - D_1 - 1/2C$

$E = B_1 - B$

$F = A - B_1$ or $A_8 - B$

$F_1 = A_1 - B_1$ or $A_3 - B$

$G = A - A_2$ or $A_8 - A_4$

$G_1 = A_1 - A_2$ or $A_3 - A_4$

$H = A_2 - B_1$ or $A_4 - B$

$L = 1/2(J_1 - K)$

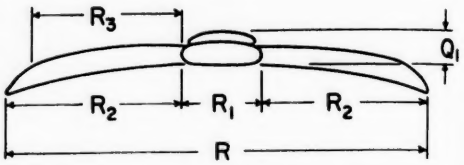
This interrelation of parts is, I believe, the strongest recommendation for placing the head in one orientation and making all measurements without change. If the measurements are all made with the line of sight perpendicular to the surface measured, then no measurements can be computed for there will be no simple relation between them, and each must be derived separately as is the case of the palpebral chord length (C_1) and the width of the chord of the posterior limb (L_1) described in this paper. While it is not inconvenient to have certain special measurements made at unusual orientations, it seems highly desirable to have most of the measurements bear some easily calculable relationships to one another.

Measurements of the thorax.—No large suite of specimens has yet been analyzed in which the thorax was preserved, so that the remarks which follow are not based on actual practice as are the discussions of the head and tail.

Total exoskeletal length (P) measured from the front end of the cephalon to rear edge of the pygidium, both in the sagittal plane.

Total thoracic length (Q) measured from the most forward exposed edge of the first thoracic segment to rearmost exposed point of the last segment in the sagittal plane. Care must be exercised to make measurements from comparable points if the head or tail is missing, for in the complete individual half of the first thoracic segment is hidden by the occipital ring of the cephalon.

Axial sagittal width of thoracic segment (Q_1) is the anterior-posterior width of an individual thoracic segment in the sagittal section. This dimension cannot be satisfactorily made on complete thoraces because of overlapping of the segments. However, if individual segments can be identified as to their correct position in the thorax (as, for example, the spinose third segments of *Olenellus*) it is suggested that a further subscript be added to indicate the segment involved, thus: Q_{13} (indicating the axial length of the third thoracic segment) (Text-fig. 12).



TEXT-FIG. *12*—Measurements of a thoracic segment.

Maximum transverse length of thoracic segment (R) measured between exsagittal planes tangent to the outer tips of the thoracic segment.

Transverse length of axial lobe (R_1) measured between exsagittal planes tangent to the outer edges of the axial lobe.

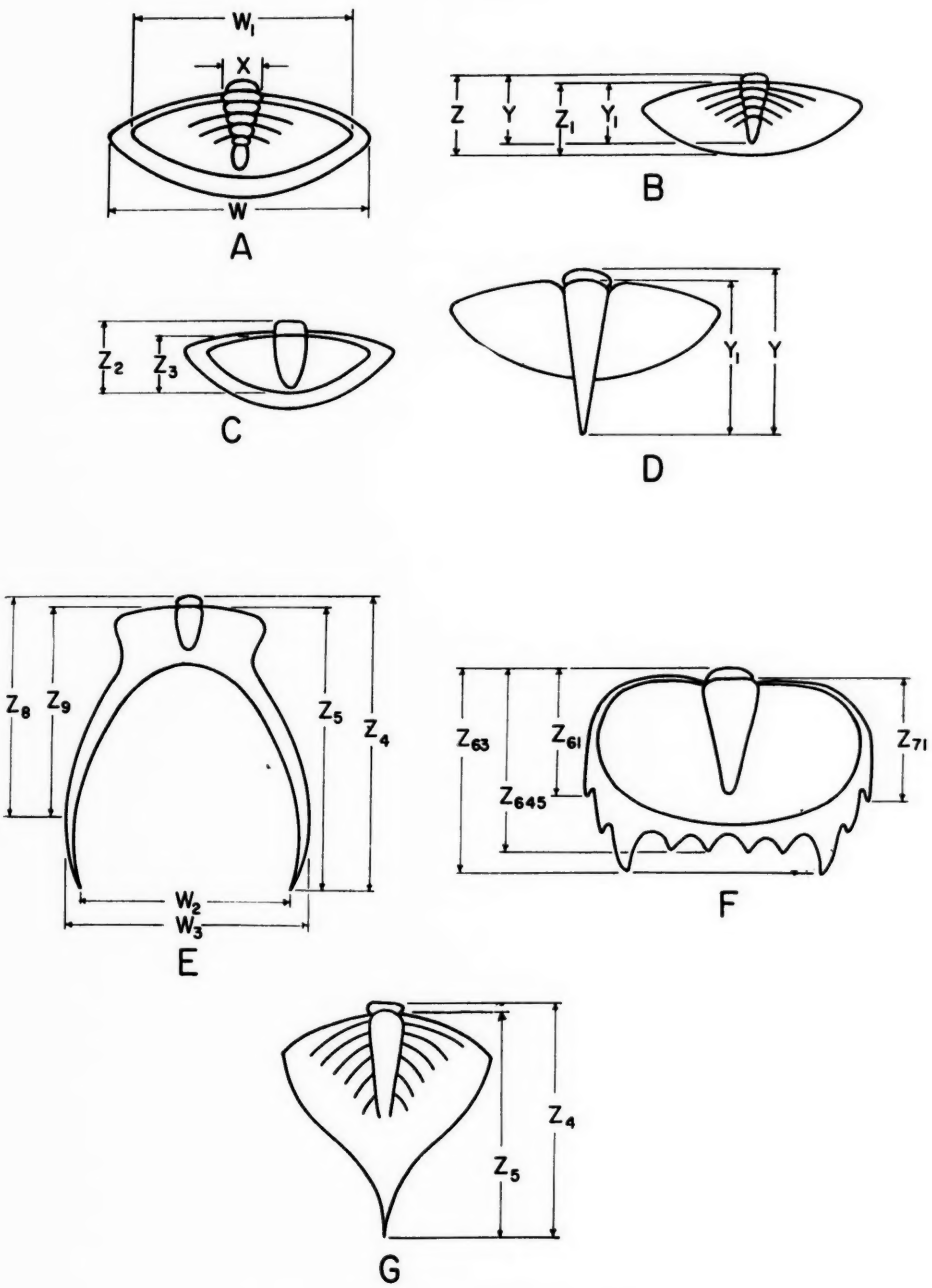
Transverse pleural length (R_2) measured between exsagittal planes tangent to the outer tip of the pleuron and the edge of the axial lobe.

Distance to point of geniculation (R_3) measured between the sagittal plane and an exsagittal plane passing through the point of geniculation. Care should be taken to state whether the latter plane is passed through the front or rear edge of the pleuron if the line of geniculation lies obliquely to the axis.

Measurements of the pygidium.—There are only four basic units on the pygidium: the length and width of the axial lobe and the length and width of the pygidium itself, but there are several variations for particular pygidial structures (Text-fig. 13).

Maximum pygidial width (W) measured between two exsagittal planes tangent to the outermost tips of the pygidium. This unit does not seem to have the common defect of maximal measures because it is of essentially constant position. In very few pygidia is the maximum point anywhere but at the anterior end.

Maximum intramarginal pygidial width (W_1) measured between two planes through



TEXT-FIG. *13*—Measurements of the pygidium.

the most distal points in the marginal furrow. This is a useful substitute for the maximum pygidial width (W) in cases where there is a well defined marginal furrow and the pygidial border is broken.

Terminal inter-spinal distance (W_2) measured between the tips of any two corresponding pairs of pygidial spines. This measure can only be used if the tips are preserved.

Maximum inter-spinal distance (W_3) measured between exsagittal planes tangent to the outer edges of the pygidial spines at their point of maximum outward deflection. In some cases the distance to this point of maximum deflection might be of value; it is described below (Z_8 and Z_9).

Anterior width of rhachis (X) measured between exsagittal planes through the dorsal furrow at points opposite the maximum lateral extension of the first segment. In this measure care should be taken not to use the articulating ring, for this part is hidden in complete specimens and frequently broken in free pygidia and is thus not as useful as the first pygidial segment.

Total length of rhachis (Y) measured from the front edge of the articulating ring to the bottom of the dorsal furrow behind the rhachis, in the sagittal plane. This unit cannot always be measured precisely because in many pygidia the dorsal furrow is not well defined posteriorly; this is an insoluble problem.

Note also that in some pygidia (*e.g.* some species of *Symphysurina*) the rhachis extends over the rear margin of the pygidium (Text-fig. 13D). There seems to me no reason for giving this case separate designation.

Intra-articulating length of rhachis (Y_1) is measured from the bottom of the furrow that marks off the articulating ring to the bottom of the dorsal furrow behind the rhachis, in the sagittal plane. This unit makes possible comparison of specimens which lack the articulating ring or in which it is covered by a thoracic segment. Furthermore, if both the total length of the rhachis (Y) and the intra-articulating length of the rhachis (Y_1) are measured it is not necessary to measure the length of the articulating ring directly, for it is equal to $Y-Y_1$. In practice I have concluded that it is not usually necessary to measure the length of the articulating ring; hence I propose no letter designation for it. I have used it on occasion, however (Shaw, 1952, p. 464, 474, etc.).

Total pygidial length (Z) measured from the front edge of the articulating ring to the rear edge of the pygidium, in sagittal section.

Intra-articulating pygidial length (Z_1) measured from the bottom of the furrow behind the articulating ring to the rear edge of the pygidium, in sagittal plane.

Intramarginal pygidial length (Z_2) measured from the front edge of the articulating ring to the bottom of the marginal furrow, in the sagittal plane.

Intra-articulating intramarginal pygidial length (Z_3) measured from the bottom of the furrow immediately behind the articulating ring to the deepest part of the marginal furrow, in the sagittal plane.

Total pygidial-spinal length (Z_4) measured from the anterior edge of the articulating ring to the tip of the pygidial spine or spines.

Intra-articulating pygidial-spinal length (Z_5) measured from the bottom of the furrow behind the articulating ring to the tip of the pygidial spine or spines.

These last two measurements are designated separately because on occasion it is possible to distinguish the total pygidial length (Z) or intra-articulating pygidial length (Z_1) by a deflection or slight furrow on the base of the spine; in such a case the separate measurements should be made.

Note also that no distinction is made between a single median spine (Text-fig. 13G) and paired lateral spines (Text-fig. 13E); none, I believe, is needed. However, distinction is necessary in the case of multipel pygidial spines.

Length of lateral pygidial spines (Z_6) measured between transverse vertical planes tangent to the front edge of the articulating ring and the tip of the spine in question. In addition, the particular spine may be indicated by adding a subscript as shown in Text-fig. 13F; thus, the length of the first spine would be designated Z_{61}, of the third would be Z_{63}. If two spines have the same length, their measurements may be combined, as in the case of spines 4 and 5 in Text-fig. 13F, thus: Z_{645}.

Intra-articulating length of lateral pygidial spine (Z_7) measured as above but with the anterior plane passing through the bottom

of the furrow behind the articulating ring, at the point where that furrow intersects the sagittal plane. A similar addition of subscripts may be used here; thus, the intra-articulating length of the third lateral spine would be Z_{73}, etc.

Distance to maximum inter-spinal distance (Z_8) measured between vertical, parallel, transverse planes tangent to the forward edge of the articulating ring and through the point of maximum lateral deflection of the paired pygidial spines (the points used to measure maximum inter-spinal distance (W_3)).

Intra-articulating distance to maximum inter-spinal distance (Z_9) measured as above but with the anterior plane passing through the point formed by the intersection of the sagittal plane and the deepest part of the furrow behind the articulating ring.

Other quantitative data on pygidia.—Besides the dimensions described above two other numerical data should be given.

1. The number of segments in the axial lobe. In stating this it should be made clear what disposition is made of the articulating ring, which is invisible or missing in many specimens, and of the terminal segment which in many species is composed of several segments fused so much as to be unrecognizable. To include either of these two units in the segment count gives an inaccurate picture and may cause confusion in comparisons with other specimens. Therefore, I suggest that the number of segments be given, excluding the articulating ring and terminal segment (Shaw, 1952, p. 473, 475, etc.).

It seems that a formula could be used to express the structure of the rhachis. Thus, "Pygidium No. 3" from the Rockledge conglomerate (Shaw, 1952, p. 475; pl. 57, fig. 16) with an articulating ring, 7 segments, and a terminal segment would be described by the formula:

A7T

If inspection of the ventral side of the pygidium should reveal that additional segments are differentiated in the terminal segment ventrally, the additional number could be indicated in parentheses after the T, thus:

A7T(+3T)

This would mean that on the ventral side 10 segments are visible in addition to the terminal lobe and the articulating ring. A number alone in parentheses

A7T(+5)

would indicate complete division of the rhachis ventrally into 12 segments without any visible ventral terminal segment.

2. Visible segments on the pleural lobes. Again the caution should be exercised to separate the terminal portion of the pleural lobe which may contain several fused segments. A similar formula may be used for this count, thus:

M4T

would indicate that the pleural lobe consists of the anterior margin, 4 segments, and the fused terminal segment. Segments visible on the ventral could be indicated in a manner similar to that described above.

M4T(+2T)

would indicate the same pleural lobe with 2 additional segments and a smaller terminal segment visible ventrally.

REFERENCES

FREDERICKSON, E. A., 1949, Trilobite fauna of the Upper Cambrian Honey Creek formation: Jour. Paleont., vol. 23, p. 341–363, pl. 68–72, 1 fig., 1 table.

GAINES, R. B., JR., 1951, Statistical study of *Irvingella*, Upper Cambrian trilobite: Texas Jour. Sci., vol. 3, p. 606–616, 1 pl., 5 fig., 2 tables.

LOCHMAN, CHRISTINA, 1947, Analysis and revision of eleven Lower Cambrian trilobite genera: Jour. Paleont., vol. 21, p. 59–71, 6 fig.

POULSEN, CHR., 1937, On the Lower Ordovician faunas of east Greenland: Meddelelser om Grönland, Bd. 119, No. 3, 72 p., 8 pl., 18 fig.

SHAW, A. B., 1950, A revision of several Early Cambrian trilobites from eastern Massachusetts: Jour. Paleont., vol. 24, p. 577–590, pl. 79, 4 fig.

——, 1952, Paleontology of northwestern Vermont. II. Fauna of the Upper Cambrian Rockledge conglomerate near St. Albans: Jour. Paleont., vol. 26, p. 458–483, pl. 5, 5 fig.

MANUSCRIPT RECEIVED MAY 28, 1956

JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 1, p. 208–214, 3 TEXT-FIG., JANUARY 1957

EOHELEA STRIDULANS, N. GEN., N. SP., A STRIKING EXAMPLE OF PARAMORPHISM IN AN AMBER BITING-MIDGE[1]

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ABSTRACT—A stridulating apparatus at the extreme end of both wings distinguishes the new species from all other known living and fossil Diptera, and must be considered a case of paramorphism. The apparatus consists of 15 parallel ridges, each provided with minute transverse ridges. Certain differences in venation and other characters necessitate erection of the new subfamily Eoheleinae in the family Ceratopogonidae.

IN STUDYING amber spiders belonging to the Mineralogical and Paleontological Museum of Copenhagen I came across a specimen of amber containing a spider and an insect in such close proximity to each other that they could not be cut apart without serious damage to the one or the other specimen. The piece was therefore cut and mounted on a single slide in such a manner that both specimens could be studied without difficulty. The spider will be described in a separate paper dealing with amber spiders of different collections and by now almost ready for print. The insect attracted my attention immediately because even under low power it exhibited plainly an organ of stridulation on each of its two wings. This was quite remarkable because the insect belonged undoubtedly to the order of Diptera none of which, whether living or fossil, were ever known to possess organs of stridulation. It is true that Recent Diptera produce sounds, but not by stridulation. Thus the amber specimen in question is an absolutely unique example and as such deserves very careful description and figuring. It is closely related to the family Ceratopogonidae (Heleidae) though differing from it in several important characters and certainly does not belong to any of the known Recent or fossil genera. For this reason I propose for it the new genus *Eohelea* and the new species *E. stridulans* the characters of which are given below.

The question of the family is more difficult to decide. The presence of stridulating organs is not in itself of sufficient value to use as a familial character because in many other insects they are commonly, though not always restricted to the male sex in closely related genera, as for example in some Orthoptera. But the difference in wing venation is sufficient to require the recognition of a new subfamily *Eoheleinae* characterized by the continuation of the costal vein beyond the tip of the wing along its posterior edge.

It is unfortunate that the specimen lacks the abdomen. The latter must have been lost through some accident in life shortly before the midge was engulfed in the still fluid resin, because I was unable to find any trace of it in the piece of amber. But the head and thorax with all appendages are well preserved as may be seen in the photograph and the drawings which were made while the piece was not yet mounted on a slide, but examined in mineral oil, rotated and propped up in the position best suited for each structure.

Subfamily EOHELEINAE, n. subfam.

Costa clearly continuing around the wing though much weaker and lighter colored along the wing's posterior edge. Metanotum without median keel or groove. Ocelli absent. Antennal flagellum with 14 segments, last four of which elongated. Only first tibiae with spurs. Third tibiae with comb of four teeth forming a single row.

Genus EOHELEA, n. gen.

Type species: *Eohelea stridulans*, n. sp.
Oligocene

Radio-medial cross-vein absent, Empodium vestigial. Second joint of scape globu-

[1] A Contribution from the Osborn Zoological Laboratory of Yale University.

lar. Each segments of flagellum with only two pairs of setae. All femora normal, cylindrical, none with spines beneath. Both wings in their apical third with a row of stridulating ridges ventral to the subcosta.

EOHELEA STRIDULANS, n. sp.
Text-fig. 1–3
Type: *E. stridulans.* Oligocene

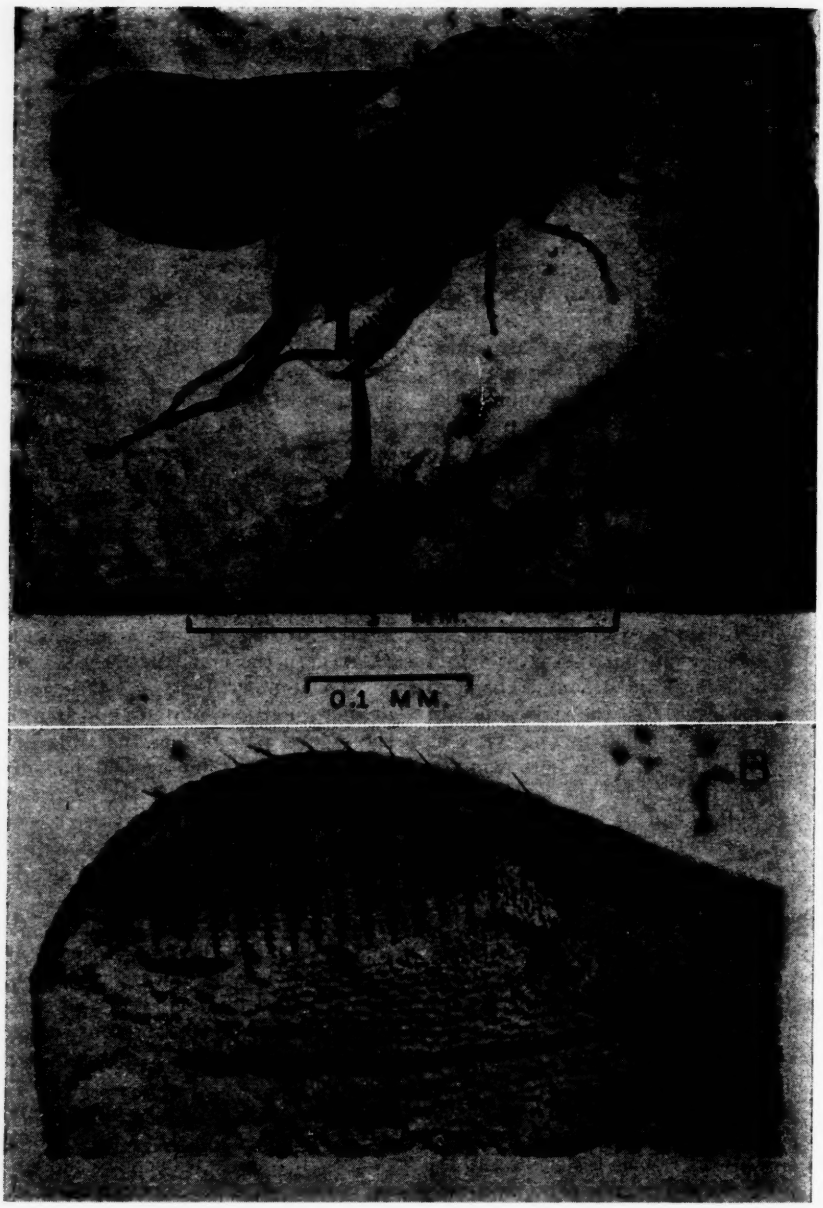
Description of holotype.—The general appearance of this fossil biting-midge may be best appreciated by an examination of the photograph which shows the insect as it appears in the amber. The wings are quite transparent and the color of the glabrous thorax fuscous and shiny. On account of the minute size of the creature it is impossible to photograph the external structure of the thorax and head in brilliant reflected light without making the wing almost invisible. A compromise between reflected and transmitted lighting had to be found by repeated experimentation to get even an approximately satisfactory picture. Because of the loss of the abdomen the exact length of the body cannot be given, but it was probably somewhere between 1 and 1.5 mm. The head is turned considerably to the right and can be therefore easily studied in face view as shown in Text-fig. 2B. The left wing is somewhat crumpled under the legs, but its stridulating ridges can be seen and studied as well as those of the right wing when one turns the slide over. The total length of the right wing is 0.83 mm., its width across the middle 0.36 mm. The total length of the left antenna is ca. 0.45 mm. The width of the head including the eyes 0.32 mm. First leg, 0.75; Second leg, 0.86; Third leg, 0.94 mm.

The compound eyes are almost, but not quite in contact with each other on the dorsal side of the head (Text-fig. 2B). Ocelli are absent. Antennae arise from the middle of the front and are composed of 16 segments the first two of which form the scape and the following 14 the flagellum. The first segment of the scape is small and cone-shaped with distinctly concave sides and truncated apex. The second segment is globose (Text-fig. 2C), compressed at both poles and with a distinct round apical depression for the reception of the base of the first segment of the flagellum, which is as long as the last one and considerably stouter. The segments of the flagellum decrease in length from the 1st to the 10th. The 11th segment is as long as the 3d; the three last segments are equally long. All segments of the flagellum have two pairs of simple setae. The segments of the scape have none. The palpi (Text-fig. 3C) are composed of four segments, the 1st and 2nd of which are supplied with a single dorsal seta, the 4th with four apical setae, while the third has none.

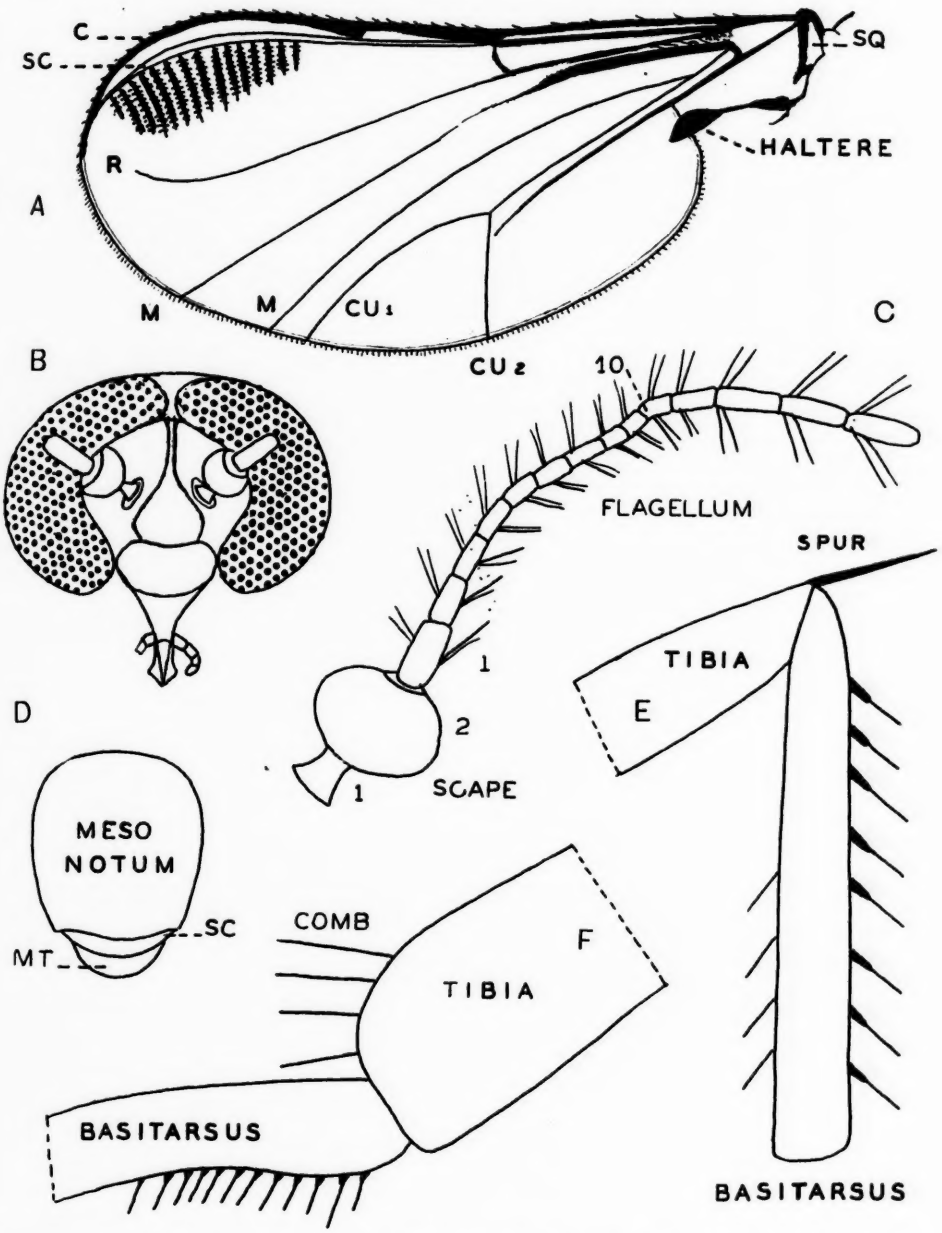
The thorax is typical. Owing to the position of the head the prothorax can be plainly seen in reflected light because almost half of its left side is fully exposed. The mesonotum is typically large, gibbous and quite glabrous without any indication of hair or setae. In dorsal aspect (Text-fig. 2D) only one transverse suture can be seen separating the large scutum from the scutellum. The metanotum is crescentic, without median keel or groove. Its surface is as smooth and glabrous as that of the mesonotum.

Except for the difference in length, the legs are very much alike. They are purposely figured at the same magnification (Text-fig. 3D–H). In the first pair the tibia is as long as the femur (Text-fig. 3D) and has a slender, sharply pointed spur at its end. In the second pair of legs the tibia is slightly longer than the femur and has no apical spur. In the third pair the tibia is slightly shorter than the femur and also has no apical spur, but is instead provided with a comb composed of a single row of 4 slender teeth (Text-fig. 2F). All three pairs of tarsi are five-jointed, their first segment, the basitarsus, by far the longest, with a ventral row of peculiar bristles thickened at base (Text-fig. 2E,F). Claws curved and smooth. A vestigial empodium is present on one of the second pair of legs (Text-fig. 3G), but absent on all other legs.

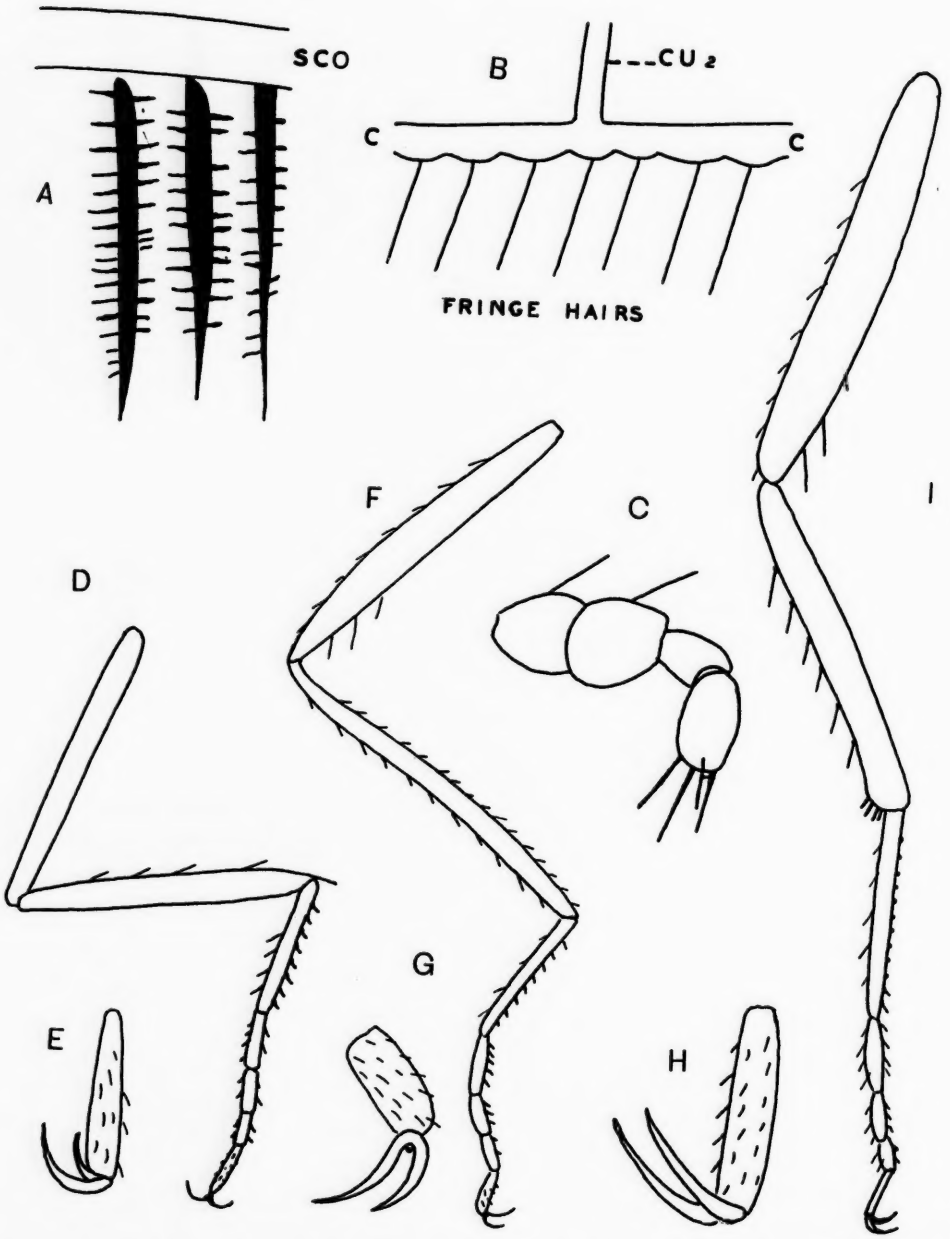
The wings are evenly rounded and broad (Text-fig. 2A). The costa is dark to the end of the wing where it becomes suddenly quite light colored and gently festooned (Text-fig. 3B) and continues in this way to the end. The dark portion of the costa is covered with small spines, the light portion with a fringe of slender hairs. There is no alula. The subcosta runs parallel to the costa and ends in the latter a little before the end of the wing (Text-fig. 2A). The radius does not quite reach the costa. The membrane of the wing



TEXT-FIG. *1—Eohelea stridulans*, n. sp. *A*, as it appears in the piece of Baltic Amber in the collections of the Museum of Mineralogy and Paleontology of Copenhagen. The three lighter spots on the head are reflections of the light and not ocelli. The specimen does not have any ocelli. The photograph was made with a micro-tessar stopped down to F. 16 so as to bring all appendages more or less into focus. ×52. *B*. Portion of the right wing of the same specimen showing the stridulating organ under higher magnification of ca. ×220. Apochromat 16 and compensation ocular ×20.



TEXT-FIG. *2—Eohelea stridulans*. n. sp. Holotype. *A*, right wing, ×120; C—costa, CU—cubitus, M—media, R—radius, SQ—squama. *B*, front view of head, ×140; only the first segment of both flagelli is shown. *C*, Left antenna, complete, ×235. *D*, Dorsal view of notum; Sc—scutellum, MT—metanotum; ×140. *E*, End of tibia with its dorsal spur and basitarsus of the first right leg, ×600. *F* End of tibia and proximal portion of basitarsus of the third left leg, ×600.



TEXT-FIG. *3—Eohelea stridulans*, n. sp. Holotype. *A*, three of the stridulating ridges, ×600; SCO—subcosta. *B*, posterior edge of wing; C—costa, CU_2—second branch of cubitus; ×600. *C*, complete left palp, ×600. *D*, first left leg, ×165. *E*, last tarsal segment with claws of the same leg, ×600. *F*, second left leg, ×165. *G*, last tarsal segment with claws of the same leg, ×600. *H*, third left leg, ×165. *I*, last tarsal segment with claws of the same leg, ×600.

is colorless and as transparent as glass, but its surface is shagreened as may be seen in the photograph, and is covered in many places with microtrichia which are visible only at high magnification and form two or three denser patches near the middle of the wing. When a beam of light strikes the wing at a certain angle, the light is reflected as by a mirror, so that the veins become scarcely visible.

The most remarkable feature of the wings is the stridulating apparatus, similarly and equally well developed on both wings. It is situated at the end of the wing, immediately under the subcosta and consists of 15 parallel ridges, the two end ones quite small (Text-fig. 2A). They are black and each is provided with a row of transverse, fine ridges (Text-fig. 3A). The actual structure of the ridges could be ascertained by an examination of sections if such sections could be made without ruining the whole specimen. But from their appearance in a certain position when the specimen is so inclined on the microscope table that the costa of the wing is higher than the fringed edge I suspect that the transverse ridges represent the edges of a row of chitinous platelets attached at about right angles to the 15 parallel ridges. Such structures have been described and figured in various Orthoptera (Petrunkewitsch & Guaita, 1901). Only in the latter the platelets are somewhat shorter than the width of the vein to which they are attached. There is also only a single stridulating vein in Orthoptera and the vibrating membrane or tympanum is usually only on the opposite wing. The necessity for the development of a membranous tympanum in an orthopteron wing is due, of course, to the fact that the first pair of wings on which the stridulating apparatus is situated, is a wing-cover rather than a wing adapted for flight, and being therefore fairly thick is unsuited for the production of sound-vibrations, while the corresponding and only pair of wings in Diptera is used for flight and is membranous. Although embryologically this pair of wings in Diptera is homologous with the wing-covers of Orthoptera, physiologically, except as regards the production of sound by stridulation, it performs the function of the second pair.

There is also another interesting and important difference between the stridulating apparatus of *Eohelea* and that of Orthoptera. In *Eohelea* it is situated at the end of the wing, in Orthoptera at the base of it. In such genera of Orthoptera as *Bradyporus* and *Ephippigera* the single stridulating vein appears to occupy the middle of the wing, but this is due to the fact that the wings in these genera are reduced to a mere rudiment sufficient to accommodate the stridulating ridge. However, besides the difference in position of the stridulating apparatus in *Eohelea* from that in Orthoptera there is also the difference in the number of stridulating ridges, in the anatomical structure of all organs and in the embryological and postembryological development from egg to adult. It is therefore impossible to derive Diptera from Orthoptera and since no other Diptera are known to possess stridulating organs the case of *Eohelea* must be regarded as the result of paramorphism (or homomorphism as some zoologists prefer to call it), i.e., of independent development of identical or highly similar organs in unrelated groups of animals. This phenomenon is well known to zoologists and paleontologists and does not need to occupy our attention here in regard to the different theoretical concepts of its origin. But it is worth while to point out that the present specimen being the only one so far discovered in an order of insects containing several thousands of species the survival value of the organ of stridulation must have been very low.

The following few references are given here in the hope that they may be of help to those who are not familiar with Diptera and with the structure of sound-producing organs in Orthoptera.

REFERENCES

BUSNEL, RENÉ GUY, 1955, Colloque sur l'acoustique des Orthoptères: INRA? Paris. 448 p. Morphologie des Appareils stridulatoire, p. 89–141; bibliography p. 401–446; 182 illustrations.

CURRAN, C. H., 1934, The families and genera of North American Diptera: 512 p. Fam. Ceratopogonidae, p. 74–77. Wing venation of 12 genera shown on p. 77.

JEANNEL, R., 1949, Insectes: vol. 9, of Traité de Zoologie, publié sous la direction de Pierre-P. Grassé, Paris. Classification et Phylogénie.

Les Insectes fossiles. Evolution et géonémie. P. 18–110; fig. 1–109.

JOHANNSEN, O. A., 1943, A generic synopsis of the Ceratopogonidae (Heleidae) of the Americas, a bibliography , and a list of the North American species: Annals Entom. Soc. Am., vol. 36, p. 763–791, pl. 1–3. Bibliography, p. 786–791.

KIEFFER, J. J., 1925, Diptères (Nématocères piqueurs): Chironomidae, Ceratopogoninaé. Faune de France, 11, p. 1–139, fig. 1–83. Paris.

MEUNIER, F., 1904, Monographie des Cecidomyidae, des Sciaridae, des Myctetophilidae et des Chironomidae de l'ambre de la Baltique: Annales de la Société Scientifique de Bruxelles. Vol. 28, mém., p. 14–275, pl. 1–16. (NB. The genera *Tanypus* and *Ceratopogon* are included in the family Chironomidae. Key to species of Ceratopogon on p. 193–197 of Annals or p. 204–208 of Mémoire. Figures of ceratopogon species on pl. 15. and 16.

PETRUNKEWITSCH, A., & GUAITA, G. v., 1904, Ueber den geschlechlichen Dimorphismus bei den Tonapparaten der Orthopteren: Zool. Jahrbücher, Abt. f. System. vol. 14, p. 292–312, pl. 15–18.

SÉGUY, EUGÉNE, 1951, Diptères: vol. 10 of Traité de Zoologie, publié sous la direction de Pierre-P. Grassé. Paris; p. 449–744. (This is a comprehensive account of the morphology, biology and classification of the order, accompanied by numerous figures. Fam. Ceratopogonidae is briefly discussed on p. 606–608).

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MAMMAL MIGRATIONS, CENOZOIC STRATIGRAPHY, AND THE AGE OF PEKING MAN AND THE AUSTRALOPITHECINES

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ABSTRACT—The larger carnivorous mammals have, on an average, greater species ranges than herbivores, and hence are particularly useful in long-distance correlation. Species ranges in the late Cenozoic appear to have been similarly distributed as in the present day. Unchecked spread of a mammal species may proceed at a pace of some 1000 km. in a century. It is thus a very exact time-marker, but its demonstration necessitates most searching ecologic and taxonomic analysis. The middle Pleistocene spread of *Crocuta crocuta* into China, Europe and Africa gives a date for Peking Man and Swartkrans ape-man coinciding with the end of the Cromerian interglacial.

INTRODUCTION

STRATIGRAPHIC zonation of terrestrial Cenozoic deposits is largely based on the changes in their mammalian faunas. The changes result from (a) extinction, (b) evolution, and (c) migration.

The weight given to each of these factors, in an attempt to determine the temporal relationships of two faunas from different localities, differs from case to case, and this is proper. But in general they can be ranked according to their importance in correlation, and then the sequence as given is one of increasing importance.

The stratigraphic significance of a faunal change is relative to its temporal and distributional rate. In the zonation of a single stratigraphic column, (a) and (c) denote points in time, whereas (b) is a gradual process. In the comparison between two stratigraphic columns, (a) loses much of its significance, for a phylum may linger on for a long time in one area, though it becomes exterminated in another. Evolution (b) is generally held to be more important; relative levels of evolution in all the phyla constituting the two faunas give fair indication of their temporal relationship In some instances the evidence from (b) has even been considered to overrule that from (c), migration. More often, however, the immigration of a new phylum at two localities is considered to be, geologically speaking, simultaneous, as long as the geographic distance between them is reasonably short. The validity of long-range correlation on this basis has been in doubt, because the time-rate of mammalian migrations has been obscure. Available data on Recent migrations and species ranges shed important light on this problem.

RATES OF MIGRATION

The migration of a species takes the form of population spread. It thus differs from such phenomena as the annual migration of birds (and some mammals and other animals); but it should be noted that some border-line cases are known, where more or less concerted mass movements do lead to the acquisition of new territories. A famous and long misinterpreted instance is that of the lemmings of northern Europe. The popular idea is that the lemmings, in years of proliferation, march to their death, the whole "army" ultimately perishing, whereas the population is carried on by the few stationary individuals. Recent studies (Kalela, 1949) have shown that this picture is largely incorrect. The lemming migrations generally lead to settlement in new areas, whereas the original territory is left with a much attenuated population. In this way the center of the population is rotated, often returning to the original area after a series of shifts.

But this is exceptional, and population spread is the common mode of migration. It results from the random movements of the individuals. The basic unit is the average distance between the birthplace of an individual and that of its parent, and the standard deviation of this distance. In prin-

ciple the movement may be in any direction; where it is directed outward from the boundary of the species range, the range is extended. It is a matter of observation that advances of the range are initiated by vagrant individuals moving outside of the settled area of the species.

Such a range extension is commonly checked by ecological barriers—physical, physiological, and others. Actual migration takes place with the removal of the barrier. This may happen in two different ways. In the first place, the barrier may be slowly retreating (say, a shift of a climatic zone, with consequent shifts of vegetational belts), and the spread of the population will keep pace with the retreat of the barrier. In the second place, there may be an ecological threshold; once it is crossed or vanishes, a large new area is open to colonization. Then an intermediate situation may be visualized: the barrier may retreat so rapidly that the species fails to catch up with it.

In the initial case, the rate of migration will be determined by the rate of change in the position of the barrier. In the two latter instances, the rate of migration depends entirely on the spreading capacity of the population.

During the Pleistocene in particular, the former mode was very common. With the advance of glaciers and the concomitant retreat of temperate biotopes, animals of arctic type spread southward. With the shrinking of ice sheets and the northward retreat of arctic biotopes, populations spread northward.

Most instances of such population spread, mainly dominated by gradual shifts of ecologic zones, probably also contain, as details in the main picture, minor instances of "threshold-effect" migration (a Recent case will be discussed below). But the most typical examples of this kind of migration occur when an obstacle is forced, bridged, or disappears. The spread will then be especially rapid if the conditions in this new area are similar to those in the original territory, because then no marked shift in the adaptation of the population is required.

What is the possible rate of such a colonization, and which mammals are especially likely to spread rapidly, and thus be particularly useful in correlation?

The study of individual migratory ranges is unfortunately still in its beginning, and most results so far have been obtained by the banding of birds and small mammals—which are generally rare as fossils and often taxonomically difficult. A good fossil record and sound taxonomy are indispensable for good results. There are however a few well-analyzed instances of present-day migration, concerning mammals of the type that are common as fossils; these have been studied particularly by Kalela (1940, 1948), whose results will be briefly summarized here.

During the time from 1880 to 1940, the polecat (*Putorius putorius*) has advanced in Finland from the Carelian Isthmus westward and northwestward to the coast of the Bothnian Gulf, as far north as central Ostrobothnia. The longest distance covered is about 450 km., and the rate of migration thus averages some 7½ km. annually, or 750 km. in a century.

As shown by Kalela, and as indicated by many other range changes during the same period (the roe deer, to be discussed below, and many bird populations), the advance is mainly a response to the climatic amelioration during this time. It should however be noted that the main direction of the advance is from east to west, not south to north; thus it seems probable that, in this special case, there may have been a threshold effect. It may perhaps be suggested that the initiation of a warmer climate permitted the population to spread from the Carelian Isthmus, whereby the road westward was opened; thus the main part of the migration later on may have been unchecked. The population was channelled in a western and northwestern direction because further northward spread was checked by a climatic barrier. The final situation, with a northern species boundary running from northwest to southeast, is simulated by many other species of animals and plants in Finland, and evidently reflects a climatic zonation.

The roe deer (*Capreolus capreolus*) has an even more spectacular migration history in about the same time. In 1850 there existed only a very small population in a limited part of Scania in southernmost Sweden (slightly south of the 56th parallel). During the 95 years up to 1945 this species has

spread into great parts of Sweden and Norway, reaching the 64th parallel and even farther north. The distance covered is 900 km. or more, and an average rate of about 1000 km. in 100 years is indicated. It should also be noted that the rate was low initially, probably because population pressure was low in the small original population, and the spread was accelerated from about 1880, when the pressure presumably mounted with population size.

The spread of the roe deer is thought mainly to depend on climatic change and the extinction of dangerous predators, particularly the wolf. Direct human activity appears to have played an insignificant role.

The seeming difference in the rate of migration between polecat and roe deer may suggest that this rate is positively correlated with size. Presumably such a correlation would not be absolute, but it is not unlikely to hold good in general. Probably, fleetness of foot and rates of reproduction are also important.

There is no reason to suppose that the polecat or the roe deer possess unusual spreading capacity. The polecat is a relatively small carnivore with a rather narrow specialization; the roe deer is highly dependent on mild winters for its subsistence. The figures would thus seem to be representative of common migration rates in mammal species. Larger and more ubiquitous mammals may be able to spread more rapidly. An unchecked spread of some 1000 km. in a century would seem a moderate estimate for most larger mammals.

This rate would mean that, under favourable circumstances, a mammalian species may migrate from the Bering Straits to western Europe in about 1000 years, a time unit which is negligible in the Cenozoic geological history. And even if the rate of 1000 km. per century would be an over-estimate, and the true rate for a species were, perhaps, only one-half or one-quarter of that, the difference would have no significance whatever in the geological time scale. Unchecked spread denotes a point in geological time. This spreading capacity appears to have been vastly underestimated in much paleontological thought.

This, it should be remembered, holds for unchecked spread only. Clearly the migration of many mammals has been much slower, and many evolving phyla have failed to colonize more than a limited area. The adaptation of most species is so narrow that optimal conditions obtain in limited areas only (and even if similar zones are available in other areas, intervening barriers may preclude migration); hence, for a colonization of new areas, evolutionary change is necessary. If the environmental gradient is steep, such a change becomes unlikely. Genetic adjustment to the different environment will often be swamped by the mother population, and only the accidental isolation of a small subpopulation is likely to lead to adaptation.

This is probably a factor which intervenes, to some extent, in all large scale migrations into great new areas. The necessary change may sometimes be effected by means of very small evolutionary steps (a single mutation in the simplest case) and the evolution will then be on the deme or subspecies level; if so, the migration will hardly be much repressed. But the adjustment may also touch many genes, and the evolution be on the species level or higher; the rate of migration would then be arrested in a roughly correlative way. Thus it is clear that the taxonomic relationship between immigrants at different sites gives important clues to the rate of migration and hence to the precision of the correlation; and the taxonomic treatment assumes the highest importance.

PRESENT-DAY SPECIES RANGES

The immigration of a single species at two localities is an event of great stratigraphic value. What is the likelihood of such an event occurring at two localities far apart, and which kinds of mammals may be especially useful in such long-range correlation?

To obtain an answer, we must first study the species ranges of Recent mammals. A study was made of some mammalian families and one subfamily typical of the modern fauna—the successful mammals of the present day. Among carnivores, the Canidae, Ursidae, and Felidae were selected, and among herbivores, the Bovidae and the Cervinae. The interest was focussed on the larger carnivores and ungulates for several reasons. In the first place, the larger mammals are not only most common and best un-

derstood in fossil faunas, but they also in general have the widest species ranges and may be especially useful in long-distance correlation. Secondly, in the Recent fauna, the taxonomy of the selected groups is fairly well worked out, and the species ranges are relatively well known. Obviously a study of rodent ranges would be of great interest, and the results would be valuable for generalizations on account of the great number of species; but rodent taxonomy is not satisfactory, and data on distribution are vague. The same holds for many other small mammals.

The ranges of distribution were computed from Ellerman & Morrison-Scott (1951); for the Ursidae, Erdbrink (1953) was used. The figures thus obtained will have some tendency to bias, giving a somewhat greater range than the actual; the distributions of most species are patchy, but more precise data can only be obtained for very few species, and the treatment should be consistent. From a paleontological point of view, in fact, the figures used here are more enlightening than very accurate estimates giving only the sum of the population "islands" within the total range.

The species which occur in the Palearctic and Indian regions were used, this being the scope of Ellerman's & Morrison-Scott's compilation, but for the species which occur also outside of these regions, the total ranges were taken. The result is probably a slight increase in group means, because endemic forms from other regions, presumably often with fairly small ranges, are left out. As the region covered is the largest land mass of the world, however, this effect can hardly be very important, and the bias is likely to be consistent.

The results are tabulated in Table 1. The species ranges are given in million square miles, in the form of frequency distributions, and the statistical parameters (arithmetic mean range and standard deviation) are entered for each distribution.

The mean ranges for species of the Canidae, Felidae and Ursidae are all approximately the same (the slight deviation for the bears lacks significance), and the similarity of the values seems to indicate that the carnivorous families tend to approach a certain general pattern of distribution. The combined figures for the three families give an estimate of this pattern.

The bovid pattern is quite different. The mean is here much lower, little more than

TABLE 1.—DISTRIBUTION OF SPECIES RANGES (IN MILLION SQUARE MILES) FOR FOUR FAMILIES AND ONE SUBFAMILY OF MAMMALS

Only species present in the Palearctic and Indian regions included

Range	Number of species					
	Canidae	Felidae	Ursidae	Canidae+ Felidae+ Ursidae	Bovidae	Cervinae
0– 1	3	0	0	3	20	8
1– 2	0	4	2	6	8	2
2– 3	1	1	0	2	4	0
3– 4	2	2	1	5	3	1
4– 5	2	0	1	3	2	1
5– 6	0	2	0	2	2	0
6– 7	2	1	0	3	1	0
7– 8	0	2	0	2	0	0
8– 9	0	1	0	1	2	0
9–10	0	0	0	0	0	0
10–15	1	4	0	5	0	2
15–20	1	1	1	3	0	1
20–25	0	0	0	0	0	0
25–30	1	0	0	1	0	0
Total	13	18	5	36	42	15
Mean range	6.8±2.1	6.8±1.1	5.9±3.0	6.7±1.0	1.8±0.3	3.7±1.3
Standard deviation	7.7±1.5	4.6±0.7	6.7±2.1	6.2±0.7	2.2±0.2	5.1±0.9

one-fourth of the carnivore mean. The cervine mean takes an intermediate position, being roughly twice the bovid mean, and half of the carnivore mean.

Like the means, the maximum ranges of carnivorous species exceed those of ungulates. The most wide-ranging carnivore (*Vulpes vulpes*) covers about three times the areas of the most widely distributed bovids (*Gazella dorcas*, *Capra ibex*) and about twice that of the three widespread cervines *Capreolus capreolus*, *Cervus elaphus*, and *Alces alces*.

This suggests that the larger carnivores will be especially valuable in long-distance correlation. It also shows that the not uncommon habit of placing populations from localities far apart in different species, simply because of the great geographic distance, is wholly unwarranted, in particular when the Carnivora are concerned.

The shape of the distributions in Table 1 is of some interest. They are more or less asymmetric and generally have a mode lower than the mean, but some appear to be bimodal or multimodal. The standard deviation is about equal to the mean. This is a character of the Poisson distribution, and a few of these distributions approach the Poisson type.

The J-pattern is most clearly seen in the bovid distribution. Here the 0–1 million square miles group is also the modal one, and the frequencies fall off regularly towards the higher values, except for a small secondary concentration in the 8–9 million square miles class. This impression still holds if the initial class is subdivided:

Species ranges	0.0–0.2	0.2–0.4	0.4–0.6	0.6–0.8	0.8–1.0
No. of bovid species	10	3	3	2	2

With still finer subdivision, of course, a decrease of frequencies to the left of the mode can be demonstrated (though the actual data are not accurate enough to permit a detailed study), for a species range cannot be infinitesimal.

The distributions for other groups depart more from the J-pattern and may suggest a combination of several different distributions. Both the combined carnivore distribution and the cervine distribution suggest three distinct modes—one with small species ranges (0–2 million square miles), another with medium ranges (3–8 million square miles) and a third with very great ranges (10 million square miles and more). This gives a division into roughly 25 per cent small-range species, 50 per cent medium-range species, and 25 per cent wide-range species among the carnivores. For the cervines, the corresponding percentages would be on the order of 65, 15, and 20 respectively; here the small-range species predominate. The bovid distribution may suggest a combination of a greatly preponderant distribution of small-range species (the range of which is extended by the great number of observations) and a small group of medium-range species; the percentages would be 95, 5, and 0.

What is the cause of the greater average and maximal ranges of carnivorous species?

The adaptation of most carnivores is broader than that of herbivores in general. A carnivorous mammal may live on many different kinds of prey, whereas most herbivores are specially adapted to certain vegetational zones.

The historical processes conducive to greater species ranges in carnivores may be visualized as follows. An ungulate species may spread into an area containing, say, two main biotopes. Optimal adaptation to each of these necessitates genetic differentiation. As long as the two populations interbreed in the marginal zone, however, such differentiation cannot become complete; there will be some gene flow across this zone. Selection acts against the gene flow, and the tendency is to build up a genetic barrier, leading ultimately to speciation.

The carnivore that immigrates into the same area will need less genetic differentiation in order to cope with the different environments, because its adaptation is more ubiquitous; consequently, the tendency to form a genetic barrier is weaker, and speciation is slow.

The result will be much the same if an otherwise uniform region is divided by a zone with different ecological conditions—say, a steppe crossed by a forest belt. The more narrowly adapted ungulate populations will be divided by this barrier, which

permits only restricted gene flow or none at all; whereas a carnivore may retain genetic contact across it. Here, too, the ungulate will speciate more rapidly than the carnivore.

Another important factor is population size. In a given area, the herbivorous mammals always outweigh the carnivorous. An ungulate population is much denser than that of a carnivore of comparable size. This leads in the first place to a much greater concentration of ungulate species with very small ranges. Most of these are relict species, the range of which has shrunk to its present size. When the number of individuals in a population is constantly held below a certain minimum, extinction is inevitable. For the ungulate population with its high density, this limit size corresponds to a smaller range than for the carnivore. Moreover the limit number will be lower because of greater facility for pairing in the dense population.

The lower population density of carnivores probably induces greater individual movement and more rapid gene flow in the population, and thus counters speciation.

Another concomitant of the lower population density of carnivorous species may also be of stratigraphic importance. Their rates of evolution may be somewhat higher than those of the large ungulate populations. There is actually some indication that this may be the case. Rates of evolution in the Equidae (Simpson, 1954) and Oreodontidae (Bader, 1955) are lower than in the Ursidae (Kurtén, 1955). For a valid generalization, however, more data are needed.

SPECIES RANGES IN THE LATE CENOZOIC

Were the distributions of species ranges for the dominant mammals of earlier epochs of the same general type as those found in present-day faunas?

No Cenozoic fauna is well enough known from all parts of the Palearctic and Indian regions to permit computation of total spe-

TABLE 2.—CARNIVORES (CANIDAE, URSIDAE, HYAENIDAE, AND FELIDAE) OF THE EUROPEAN AND CHINESE LOWER PLIOCENE

	Europe	China
Canidae	*Amphicyon pyrenaicus*	(*Amphicyon* sp.)
	Simocyon primigenius	*Simocyon primigenius*
	Metarctos diaphorus	
Ursidae	*Indarctos ponticus ponticus*	*Indarctos ponticus lagrelii*
	Indarctos atticus	(*Agriotherium* sp.)
	Ursavus depereti	
Hyaenidae	*Crocuta eximia eximia*	*Crocuta eximia variabilis*
		Ictitherium gaudryi
	Ictitherium robustum	
	Ictitherium hipparionum hipparionum	*Ictitherium hipparionum wongii*
		Ictitherium hyaenoides
	Hyaenictis graeca	
	Lycyaena chaeretis	
Felidae	*Machairodus aphanistus aphanistus*	*Machairodus aphanistus palanderi*
		Machairodus tingii
	Epimachairodus taracliensis	
	Paramachaerodus orientalis orientalis	*Paramachaerodus orientalis maximiliani*
		?Megantereon sp.
	Metailurus parvulus parvulus	*Metailurus parvulus* minor
		Metailurus major
	Felis attica	(*Felis* sp.)
	Felis neas	

Notes: *Indarctos lagrelii* is clearly close enough to *I. ponticus* to be considered the same species; the distinction was mostly based on the geographic distance. The same holds for *Crocuta variabiiis* (see also Orlov, 1941), *Ictitherium wongii* (see Kurtén, 1954b), and *Machairodus palanderi* and *Paramachaerodus maximiliani* (see Pilgrim, 1931), as compared with their European allies. The relationships between "*Felis leiodon*," "*Machairodus*" *parvulus*, and *Metailurus minor* have been cleared up by Thenius (1951). *Indarctos sinensis* is probably a male of the species of which the type of *I. lagrelii* represents the female; the sex dimorphism would be the same as in other large bears (see Kurtén, 1955). Several European "species" of *Indarctos* may represent sexual and individual variants.

Important literature includes Pilgrim (1931) and Zdansky (1924).

cies ranges, and a different approach is necessary. The method is now to select some well-documented faunas and study their representatives at localities relatively far apart, ascertain the number of species common to both areas and compute their relative frequency. Comparison with Recent conditions will indicate to what extent the distributions conserve their pattern through time.

I have selected the European and Chinese faunas of the Pontian (lower Pliocene), of the Cromerian (Günz-Mindel interglacial), and of the latest Pleistocene. The groups studied are the Canidae, Ursidae, Felidae, and Hyaenidae (the last-mentioned group was not considered in the study of the Recent distributions because it has so few surviving members). The comparisons are given in Tables 2–4; the appended notes give references and some brief explanations of the taxonomic treatment where it differs from previous opinions. Some species of uncertain status have not been included.

The number of species known in Europe and China, respectively, at different times is given under N_1 and N_2 in Table 5, and the number of species common to both areas under C. The Chinese forms bracketed in Table 2 are not included in the tabulation, because of their uncertain status. In the figures for the latest Pleistocene, all the Recent species of Table 4 were also included, though in many cases their presence in these areas has not been established.

Simpson (1947) has shown that the formula

$$\frac{100\,C}{N_1},$$

in which C is the number of species common to both faunas, and N_1 the number of species known in the smaller of the two faunas (thus, the percentage of common species in the smaller fauna), is the best simple measure of taxonomic resemblance. (Because of the denominations in Table 5, we have to substitute N_2 for N_1 in one instance, for the early Pliocene, where $N_1 > N_2$).

These percentages are of the same order of magnitude throughout, indicating that patterns of distribution have been stable. The Recent percentage of common forms is

TABLE 3.—CARNIVORES (CANIDAE, URSIDAE, HYAENIDAE, AND FELIDAE) OF THE EUROPEAN AND CHINESE CROMERIAN

	Europe	China
Canidae	*Cuon priscus*	*Cuon alpinus antiquus*
	Canis lupus mosbachensis	*Canis lupus variabilis*
		Canis cyonoides
	Vulpes vulpes angustidens	*Vulpes vulpes* subsp.
		Vulpes corsac
	Alopex sp.	
	Lycaon lycaonoides	
		Nyctereutes megamastoides
Ursidae	*Ursus arctos deningeri*	*Ursus arctos* subsp.
	Ursus thibetanus schertzi	*Ursus thibetanus kokeni*
Hyanidae	*Hyaena perrieri mosbachensis*	
	Hyaena brevirostris brevirostris	*Hyaena brevirostris sinensis*
	Crocuta crocuta subsp.	*Crocuta crocuta ultima*
Felidae	*Homotherium crenatidens crenatidens*	*Homotherium crenatidens ultimum*
		Megantereon inexpectatus
	Felis leo	
		Felis tigris
	Felis pardus	*Felis pardus*
	Felis lynx issiodorensis	*Felis ?lynx teilhardi*
	Felis silvestris	
		"Felis "microtus"
		Acinonyx sp.

Notes: On the Hyaenidae, see Kurtén (1956). Full data on the Ursidae will be published elsewhere; see also Erdbrink (1953). The Canidae have been revised recently by Thenius (1954). The Cromerian *Homotherium* can hardly be distinguished specifically from the Villafranchian *H. crenatidens*, of which it is a direct descendant; and this, in turn, cannot be validly separated from *H. ultimum*. *Felis teilhardi* is tentatively assigned to *F. lynx*.

Important literature includes Kretzoi (1937), Pei (1934), Zdansky (1925, 1928), and Zeuner (1937).

TABLE 4—CARNIVORES (CANIDAE, URSIDAE, HYAENIDAE, AND FELIDAE) IN THE RECENT FAUNAS OF EUROPE AND CHINA, WITH INCLUSION OF LATEST PLEISTOCENE FORMS (P)

	Europe	China
Canidae	*Cuon alpinus* (P)	*Cuon alpinus*
	Canis lupus	*Canis lupus*
	Canis aureus	
	Alopex lagopus	
	Vulpes vulpes	*Vulpes vulpes*
	Vulpes corsac	*Vulpes corsac*
	[*Nyctereutes procyonides*][1]	*Nyctereutes procyonides*
Ursidae	*Ursus arctos*	*Ursus arctos*
		Ursus thibetanus
	Ursus spelaeus (P)	
Hyaenidae	*Crocuta crocuta spelaea* (P)	*Crocuta crocuta ultima* (P)
	Hyaena hyaena monspessulana (P)	*Hyaena hyaena hyaena*
Felidae	*Felis silvestris*	
		Felis bieti
		Felis chaus
		Felis manul
	Felis lynx	*Felis lynx*
		Felis temmincki
		Felis bengalensis
		Felis nebulosa
	Felis pardus "spelaea" (P)	*Felis pardus* subsp.
	Felis leo spelaea (P)	
		Felis tigris

[1] Introduced.

Notes: Data for living species are from Ellerman & Morrison-Scott (1951). On the Hyaenidae, see Kurtén (1956). The name *Felis pardus spelaea* is invalid by homonymy with *F. leo spelaea*.

somewhat lower; this may be the result of the activity of man.

Another formula,

$$\frac{100\,C}{N_1+N_2-C}$$

may also be used for such a comparison, but its use presupposes that we have complete knowledge of the two faunas to be compared, which is improbable for all except the Recent faunas. The fossil records are however fairly good, especially for the Pleistocene. There is a sharp drop from the the Pleistocene to the Recent in this measure, resulting from the extinction of *Cuon alpinus* and the hyenas in Europe. The percentages for the fossil faunas are again approximately constant, and the consistent trend in the two measures indicates that the results are valid.

It may thus be concluded that the species ranges of larger carnivores have been comparable to those in the present day as far back as in the Pliocene and thereafter; if anything, they may have averaged slightly greater than today.

Both China and Europe belong to the same great faunal region. For the sake of completeness some comparison should also be made between regions nowaday char-

TABLE 5—NUMBER OF SPECIES OF CANIDAE, URSIDAE, HYAENIDAE, AND FELIDAE IN CONTEMPORARY DEPOSITS OF EUROPE AND CHINA (N_1, N_2), AND NUMBER OF SPECIES COMMON TO BOTH (C), FROM TABLES 2–4; WITH COMPARISONS OF RELATIVE FREQUENCIES OF COMMON SPECIES

	Europe (N_1)	China (N_2)	Common (C)	$\frac{100\,C}{N_1}$ or $\frac{100\,C}{N_2}$	$\frac{100\,C}{N_1+N_2-C}$
Recent	8	17	4	50	19
Late Pleistocene	14	18	9	64	39
Cromerian	15	17	9	60	39
Early Pliocene	17	12	7	58	32

acterized by markedly different faunal facies. I have selected the Indian and European faunas of the Pontian, the Villafranchian, and the present day.

The Siwaliks equivalent of the Pannonian, or Pontian sensu lato (Vallesian +Pikermian of the Spanish succession) is the Chinji+Nagri (Colbert, 1935). These contain at least 12 species of the Canidae, Hyaenidae, (Ursidae)[2] and Felidae. Of these, only one (*Crocuta eximia latro*) can at present be identified with any European species.[3] The possible identity of *Amphicyon palaeindicus* (with the synonyms *A. sindiensis*, *A. pithecophilus*) with a contemporary European ally cannot be excluded, but this must await a revision. The frequency of common species would thus be 8 per cent.

Of 13 species present in the Pinjor zone of the Siwaliks, one (*Hyaena brevirostris neglecta*) appears to be conspecific with a European Villafranchian form, the nominate subspecies (Kurtén, 1956). Another, "*Sivafelis*" *brachygnathus*, seems likely to be conspecific with the European Villafranchian cheetah, *Acinonyx pardinensis*, according to Matthew (see Colbert, 1935). The frequency of common species may thus be around 15 per cent.

In the present-day fauna of India, 23 species of these carnivorous families are represented. Four of them (*Canis lupus*, *Canis aureus*, *Felis lynx*, *Ursus arctos*) are identical with European species. The percentage 100 C/N_1 is thus 50, as in the comparison between Europe and China. A continued rise in the frequency of common species from the Pliocene to the Recent is indicated.

Application of the other measure, 100 C/N_1+N_2-C, gives roughly the following percentages: Pontian 4; Villafranchian 10; Recent 15. The trend is similar.

This might mean that species ranges have extended gradually during the period covered; or it may simply mean that the isolation of the Indian region has been gradually reduced—thus a special case without real bearing on the problem under consideration. In view of the apparent constancy of the European/Chinese indices for the same period, the latter interpretation appears more probable.

Similar comparisons of earlier Tertiary faunas would be of great interest, but they are beyond my competence. The tendency to create new species simply because of great distances between different localities will too often confuse the issue, and adequate revision of much of the material is necessary before valid comparisons can be made. From the fact that climatic zonation seems to have been, less pronounced in the early Tertiary than in the Neogene, Pleistocene, and postglacial, it may perhaps be predicted that species ranges will be found to have averaged as great in the early Tertiary as now, or greater, and that distant localities will have a high frequency of common species.

In such revision the guiding principle should be the biological species concept, by means of population analysis, and the null hypothesis of the statistician. Preoccupation with analysis, at the cost of synthesis, has been prevalent since the turn of the century, and has sometimes led to almost fantastic feats of misinterpretation. Schindewolf's (1954) diatribe against "die alles vernünftige Mass übersteigende Arten-, Gattungs- und Namenmacherei, die vielfach als reiner Selbstzweck erscheint," is timely, and his espousal of the "new systematics" with its synthetic approach is laudable. A desirable result would be the reinstating of the species as the basic taxonomic category in paleontology, instead of the genus, which now masquerades in that role—often enough because it is actually doing the work of the species or the subgenus.

PLEISTOCENE PROBLEMS

Pleistocene stratigraphy, insofar as it is based on mammalian faunas, to a great extent relies on the migration phenomenon. The species is too long-lived to be used as a horizon marker when the stratigraphic zones represent much shorter time spans

[2] The Ursidae are not represented in the Pontian, but they are present in later faunas. On Siwalik faunas, see Pilgrim (1932), Colbert (1935).

[3] *Crocuta mordax* Pilgrim is a synonym of *C. "gigantea" latro* Pilgrim, as has also been suggested by Colbert (1935). The relationships of the middle Siwaliks hyenas are too complex to be discussed here; a revision is in progress.

than the average longevity of species. Relative level of evolution within the scope of a species may be used over short geographic distances, but long-range correlation on this basis may be spurious. Geographic subspeciation may completely simulate temporal subspeciation, and thus a form may have a more advanced facies in one area than in another, in spite of perfect contemporaneity. As an example may be noted that the subfossil badgers (*Meles meles*) of Denmark are similar to the living Swedish badgers, whereas the living Danish population is of a more progressive type, with much lengthened crushing talonid in M_1 (Degerböl, 1933; Kurtén, 1954a).

Instead, correlation within type areas is based on a combination of this criterion with that of migration. The main interest is directed to the type of migration which is dominated by secular shifts in climate, and and the faunas are interpreted as representing cold or warm stages. Correlation between distant areas with the same type of climatic history, say Europe and North America, is based on the assumption that the climatic oscillations were synchronous in both. But between glaciated and periglacial areas on one hand, and areas with a pluvial-dry oscillation on the other, the correlation becomes increasingly uncertain.

The only faunal event which may offer a solution seems to be the unchecked spread of a new, highly ubiquitous species into both areas. From the previous discussion it is clear that we may most hopefully look to the larger carnivorous forms to supply such evidence. One such instance, which furnishes a middle Pleistocene datum line, will be discussed here.

THE BREVIROSTRIS-CROCUTA TRANSITION

In the Cromerian, or Günz-Mindel interglacial, the spotted hyena (*Crocuta crocuta*) replaces its ecological predecessor, *Hyaena brevirostris*, in Europe. The same transition occurs in Asia, and moreover records from Africa show *C. crocuta* to have been a Pleistocene immigrant in this continent. Details of the history are given in Kurtén (1956), and only a brief review, with some additional information, is necessary here.

Hyaena brevirostris Aymard is a gigantic member of the genus *Hyaena*, fairly closely related to the living *H. brunnea*. It occurs in the Villafranchian and Cromerian of Europe; in the Pinjor zone of the Siwaliks; in the Villafranchian and middle Pleistocene of China; and in the Djetis zone of Java.

Crocuta crocuta (Erxleben), the living spotted hyena, had a very great range of distribution in the Pleistocene, seemingly not much inferior to the territories of the living *Ursus arctos*, *Canis lupus*, and *Vulpes vulpes*. In Europe the species makes its first appearance in the Cromerian; in China it appears first in the middle Pleistocene of Choukoutien and correlative localities. The earliest record in Africa is from the australopithecine site of Swartkrans.

The probable ancestor of the spotted hyena is *Crocuta sivalensis* (Falconer & Cautley) from the Pinjor zone of the Siwaliks, India.

Both in Europe and in China the immigration of *Crocuta crocuta* is associated with the extinction of *Hyaena brevirostris*. Some conclusions about the nature of this replacement seem to be warranted.

The replacement of one species by another, ecologically related species may occur in several ways:

(1) The extinction of the earlier form has no causal connection with the immigration of the later form. Both events result from the action of other factors, for instance climatic. This type of replacement is common in the Pleistocene.

(2) The extinction of one species permits the subsequent immigration of another.

(3) The immigrating form is adaptively superior to the local form, and ousts it through competition.

These possibilities may be combined in various ways. They have very different stratigraphic value. It is clear that many types of replacement depend entirely on local factors and thus are unlikely to provide tools for long-distance correlation between localities with different facies. What we require is a replacement of type (3), with the qualification that the migrant should be superior to the local form in all the realized environments, as well as capable of rapid spreading. It is suggested that the *brevirostris-crocuta* replacement is of this type.

The actual history of the replacement in

a local fauna is best recorded at Choukoutien (Pei, 1934). *Hyaena brevirostris* is confined to the deposits below the Peking Man level; *Crocuta crocuta* to those above that level. It is possible that the two forms existed together for a short time in this area; it is improbable that they did so for a prolonged period.

The correlative Chinese deposits show that both hyenas were at this time associated with an otherwise homogeneous fauna (the *Ailuropoda-Stegodon* fauna). This funa covers a great range from Indochina to northeastern China, and there is, of course, some regional differentiation, but that is all. There is no regional replacement of the two hyenas: they occur at random, one species or the other, scattered throughout this wide area. The replacement does not thus appear to be associated with any environmental change, and the suggestion is clearly that it was an internal affair between the two hyaenids: that *Crocuta* replaced *Hyaena* by competition.

In Europe the same replacement is enacted in a totally different setting. Apart from a few wide-ranging species, the fauna is quite distinct, and the environment probably highly different, from that in east Asia. The replacement of *Hyaena brevirostris* by *Crocuta crocuta* is recorded from the Forest Bed in East Anglia (Zeuner, 1937), Süssenborn in Germany (Soergel, 1936), and Gombaszög in Hungary (Kretzoi, 1937). These localities are comparatively close to each other and must be considered as belonging to a single narrowly defined faunal province; there was at that time ample land connection between them. The difference in time between the immigration of *Crocuta crocuta* in Hungary and in East Anglia cannot reasonably have amounted to more than a few centuries (more probably a few decades) which, geologically speaking, is a most gratifying precision.

This evidence necessarily overrules indications to the contrary from relative level of evolution in small mammals, which may show geographic subspeciation within the range, and small differences in faunal composition reflecting local biotopes. Supposed differentiation among larger mammals appears to be spurious. The brown bears from these three localities, for instance, have been placed in different species: Soergel (1926) erected the "species" *Ursus süssenbornensis* for the Süssenborn form; Andrews (1922) based another "species," *Ursus savini*, on the Forest Bed sample; while Kretzoi (1937) placed the Gombaszög bear in *Ursus etruscus* as a distinct subspecies. The differences are imaginary, and all these populations belong in the single subspecies *Ursus arctos deningeri* von Reichenau, which is also known from other localities of Cromerian age.

The Forest Bed underlies the dichotomous Lowestoft (= Mindel) glaciation. Since the *brevirostris-crocuta* replacement apparently occurs within the Forest Bed, it must antedate Mindel I. The Süssenborn horizon with *H. brevirostris* and *C. crocuta* is regarded as representing the oncoming Mindel I or II; the former alternative must clearly be accepted. This fixes the time of the replacement within rather narrow boundaries; it must have occurred toward the end of the Cromerian interglacial, shortly before the beginning of Mindel I. Zeuner (1937) records *C. crocuta* from the Cromer Forest Bed, which is thought to be early Cromerian. I have not seen any specimen from there; those handled by me are *C. crocuta* from Palling and West Runton, and *H. brevirostris* from Palling and Mundesley; moreover a fine jaw of *H. brevirostris* from Bacton in a private collection, of which Dr. E. Ellis (Norwich) has kindly sent me a photograph. Some excellent teeth of *C. crocuta spelaea* from Corton Cliff may originate from the Corton Sands, which postdate the Cromerian (this was suggested by Dr. R. West, personal communication).

The faunas from Mauer and Mosbach, which would seem to represent a central level in the Cromerian, lack *C. crocuta;* the hyena is a late survival of *H. perrieri.* If the record from Cromer is correct, it may indicate that the sequence there may actually span the whole interglacial, and not only the earlier part of it.

Since *Hyaena brevirostris* is known from Europe, China, India, and Java, it is clear that the species was adaptable to many different climates and biotopes. It seems therefore that biotic factors would be more important in its extinction than abiotic. Furthermore, as far as we know, there was

no common abiotic factor in all these areas; but a biotic change common to them all, except Java, is the immigration of the prospective competitor *Crocuta crocuta*. The only reasonable interpretation is that the giant *Hyaena* was ousted by the immigrant.

We do not know what advantage the spotted hyena may have had over *H. brevirostris*. But the spread of *C. crocuta* occurred subsequent to an evolutionary change from a more primitive to a more specialized condition. The probable ancestor of the species, the Villafranchian *C. sivalensis*, had a larger M^1 and a longer talonid in M_1. The reduction of these elements eliminates the chopping part of the bite and extends the slicing part. This improvement may seem ridiculously small to account for so decisive a change in the relation between two species; but it may have been sufficient to tip the scales and change the pattern of interspecific selection. Even very small selective advantages have been shown by population geneticists to be of far-reaching importance. It would appear that *Crocuta sivalensis* was able to hold its own in competition with *Hyaena brevirostris* in the Indian region, in Villafranchian time, but not outside of that local biotope; whereas its more progressive descendant attained superiority and migrated out into the Palearctic and Ethiopian regions, ousting and supplanting *Hyaena brevirostris* throughout the area of that species.

THE AGE OF PEKING MAN AND THE AUSTRALOPITHECINES

A form spreading from India will have approximately equal distances to travel to Korea, Europe, and north Africa. An unchecked spread at the average pace of 1000 km in a century (which, as we have seen, is a moderate estimate for an animal of this type) would carry the species into these areas in a matter of five centuries. The pragmatic evidence for the great adaptability of *C. crocuta* indicates that the spread was mainly of the unchecked type. Some retardation may however have occurred as a result of population pressure from the competing form, *H. brevirostris*. Still it is likely that the duration of this spread was very short, a small fraction of the Cromerian interglacial at most.

This appears to give a reliable and very exact date for the Peking Man level at Choukoutien, which may be correlated with the late Cromerian interglacial in Europe. Peking Man is thus very slightly younger than Heidelberg Man from Mauer (middle of Cromerian interglacial). A date roughly equivalent with the Cromerian has also been suggested by Pei (1939).

The arrival of *C. crocuta* in South Africa probably also occurred at the same time, or at the beginning of the Mindel glaciation at the latest. The possibility of a separate migration to South Africa, antedating that into the Palearctic region, should not be overlooked, considering that *H. brevirostris* did not reach South Africa. However, the giant *Hyaena* was almost certainly present in the Persian region (judging from its established presence in both India and Europe in Villafranchian time), which constitutes the route from India to Africa, and hence a separate, earlier migration along this route seems improbable.

This it may be concluded that Swartkrans is equivalent with the early Mindel in Europe, or the late Cromerian at earliest. Kromdraai is later than Swartkrans, but no exact date can be given; it would hardly seem to be younger than the following interglacial (Holstein, Swanscombe, Mindel-Riss). Sterkfontein and Makapan are earlier, and may be anything from late Villafranchian to early Cromerian.

This date is slightly later than what has generally been assumed for the australopithecines (many students place all of them in the Villafranchian or even earlier) but at present no other species disproves the suggested correlation, and Dr. R. F. Ewer of Grahamstown (personal communication) kindly informs me that this dating may be accepted for the remainder of the fauna. Swartkrans ape-man is thus a contemporary of Heidelberg Man and Peking Man.

Finally, the presence of *Hyaena breevirostris* in the Djetis zone may give some information on the age of Modjokerto Man. This is however much less exact, since *C. crocuta* did not reach Java and the gaint *Hyaena* may have lingered on in this region

to a later date. The only suggestive fact is the intermediate character of the Javan subspecies *H. brevirostris bathygnatha* (Dubois), as compared with the Villafranchian *H. brevirostris licenti* (Pei) and the Cromerian *H. brevirostris sinensis* (Owen) of China (see Kurtén, 1956), which might indicate an intermediate date, perhaps late Villafranchian; but, as previously noted, such evidence may be highly misleading.

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REFERENCES

ANDREWS, C. W., 1922, Note on a bear (*Ursus savini* sp. n.) from the Cromer Forest-Bed: Ann. Mag. Nat. Hist., London, vol. 9, p. 204–207.

BADER, R. S., 1955, Variability and evolutionary rate in the oreodonts: Evolution, vol. 9, p. 119–140.

COLBERT, E. H., 1935, Siwalik mammals in the American Museum of Natural History: Am. Philos. Soc., Trans., new ser., vol. 26 p. x+401 p.

DEGERBÖL, M., 1933, Danmarks, pattedyr i fortiden i sammenligning med recente former (with an English summary): Vid. Meddel. Dansk Nat. hist. Forening, vol. 96, Festskrift 2, p. 357–641, pl. 12–24.

ELLERMAN, J. R., & MORRISON-SCOTT, T. C. S., 1951, Checklist of Palaearctic and Indian mammals, 1758 to 1946: British Mus. (Nat. Hist.), p. 1–810.

ERDBRINK, D. P., 1953, A review of fossil and Recent bears of the Old World: 597 p., 22 pl. Deventer.

KALELA, O., 1940, Über die Einwanderung und Verbreitung des Iltis, *Putorius putorius* (L.), in Finnland: Ann. Acad. Sci. Fennicae, ser. A., vol. 54, no. 6, p. 1–76.

——, 1948, The occurrence of roe deer in Finland and changes in its distribution in the adjoining areas (in Finnish, with an English summary): Suomen Riista, 1948, no. 3, p. 34–56.

——, 1949, Über Fjeldlemming-Invasionen und andere irreguläre Tierwanderungen: Ann. Zool. Soc. "Vanamo," vol. 13, no. 5, p. i-iv, 1–90.

KRETZOI, M., 1937, Die Raubtiere von Gombaszög nebst einer Ubersicht der Gesamtfauna: Ann. Mus. Nat. Hungarici, pars min. geol. paleont., vol. 31, p. 88–157, pl. 1–3.

KURTÉN, B., 1954a, Observations on allometry in mammalian dentitions; its interpretation and evolutionary significance: Acta Zool. Fennica, no. 85, p. 1–13.

——, 1954b, The type collection of *Ictitherium robustum* (Gervais ex Mordmann) and the radiation of the ictitheres: Acta Zool. Fennica, no. 86, p. 1–26.

——, 1955, Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüler and Heinroth. Acta Zool. Fennica, no. 90, p. 1–48.

——, 1956, The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto: Am. Mus. Novitates, no. 1764, p. 1–48.

ORLOV, J. A., 1941, Tertiary Carnivora of West Siberia. IV. Hyaeninae: Trav. Inst. Paléont. URSS, vol. 8, no. 3, p. 40–60, 5 pl.

PEI, W. C., 1934, On the Carnivora from locality 1 of Choukoutien: Paleont. Sinica, ser. C, vol. 8, no. 1, p. 1–116, pl. 1–24.

——, 1939, Geochronological table no. 1, an attempted correlation of Quaternary geology, palaeontology and prehistory, in Europe and China: Univ. London, Inst. Arch., Occ. Pap., no. 2, p. 1–16.

PILGRIM, G. E., 1931, Catalogue of the Pontian Carnivora of Europe in the department of geology: p. i-vi, 1–174, 2 pl., Brit. Mus. (Nat. Hist.).

——, 1932, The fossil Carnivora of India: Palaeont. Indica, new ser., vol. 18, p.1 –232, pl. 1–10.

SCHINDEWOLF, O. H., 1954, Zur taxonomie rezenter und fossiler Organismen: C. R. Congr. Géol. Int. Alger 1952, no. 19, p. 81–91.

SIMPSON, G. G., 1947, Holarctic mammalian faunas and continental relationships during the Cenzoic: Geol. Soc. Am., Bull., vol. 58, p. 613–688.

——, 1954, The major features of evolution: Columbia Biol. Ser. no. 17, xx+434 p.

SOERGEL, W., 1926, Der Bär von Süssenborn. Ein Beitrag zur näheren Kenntnis der diluvialen Bären: Neues Jahrb. ser. B, Beil.-Band 54, p. 115–156, pl. 3–14.

——, 1936, *Hyaena brevirostris* Aymard und *Hyaena* ex aff. *crocotta* Erxl. aus den Kiesen von Süssenborn: Zeitschr. deutschen geol. Gesell., vol. 88, p. 525–539, pl. 45–48.

THENIUS, E., 1951, Zur odontologischen Charakteristik von "*Felis*" *leiodon* aus dem Pont von Pikermi (Griechenland): Neues Jahrb., Jahrg. 1951, no. 3, p. 88–96.

——, 1954, Die Caniden (Mammalia) aus dem Altquartär von Hundsheim (Niederösterreich) nebst Bemerkungen zur Stammesgeschichte der Gattung *Cuon:* Neues Jahrbuch, Abh., vol. 99, no. 2, p. 230–286.

ZDANSKY, O., 1924, Jungtertiäre Carnivoren Chinas: Palaeont. Sinica, ser. C. vol. 2, no. 1, p. 1–155, pl. 1–33.

——, 1925, Quartäre Carnivoren aus Nord-China: Palaeont. Sinica, ser. C, vol. 2, no. 2, p. 1–30, pl. 1–4.

——, 1928, Die Säugetiere der Quartärfauna von Chou-k'ou-tien: Paleont. Sinica, ser. C, vol. 5, no. 4, p. 1–146, pl. 1–16.

ZEUNER, F. E., 1937, A comparison of the Pleistocene of East Anglia with that of Germany: Prehist. Soc. Cambridge, Proc., new ser., vol. 3, p. 136–157.

MANUSCRIPT RECEIVED JUNE 11, 1956

JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 1, 228–241, 6 TEXT-FIG., JANUARY 1957

THE STATUS OF THE UPPER PLIOCENE TURTLE, *TESTUDO TURGIDA* COPE

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ABSTRACT—Two type specimens of turtles from Pliocene deposits, *Testudo turgida* Cope, 1892 and *Testudo riggsi* Hibbard, 1944, are redescribed and illustrated. Additional specimens of *Testudo riggsi* show similarities with *Testudo turgida* and are therefore placed in synonomy. The additional specimens aid in determining the generic placement of these turtles which had previously been considered to be *Gopherus* by Williams in 1950.

INTRODUCTION AND ACKNOWLEDGMENTS

SMALL land turtles, of similar size and characteristics, under two distinct names from deposits of Pliocene age in Texas and Kansas previously described as two species are considered synonymous. The generic placement of these two turtles, *Testudo turgida* Cope, 1892 and *Testudo riggsi* Hibbard, 1944, was challenged by Williams in 1950, who placed both of them in the genus *Gopherus*. Reexamination of the specimens and associated materials, plus additional new material, confirms their synonymy and suggests a return to the original placement in the genus *Testudo*.

This investigation was made possible through the generosity of the following individuals and institutions who loaned or allowed examination of specimens in their care: E. H. Colbert, American Museum of Natural History; Norman Hartweg, Museum of Zoology, University of Michigan; Claude W. Hibbard, Museum of Paleontology, University of Michigan; Jack Hughes, Panhandle Plains Historical Museum; Horace G. Richards, The Academy of Natural Science of Philadelphia; J. A. Wilson, University of Texas and R. W. Wilson, University of Kansas Museum of Natural History. The author also wishes to thank Claude W. Hibbard for the use of facilities, for criticism and advice.

SYSTEMATIC PALEONTOLOGY

TESTUDO TURGIDA Cope

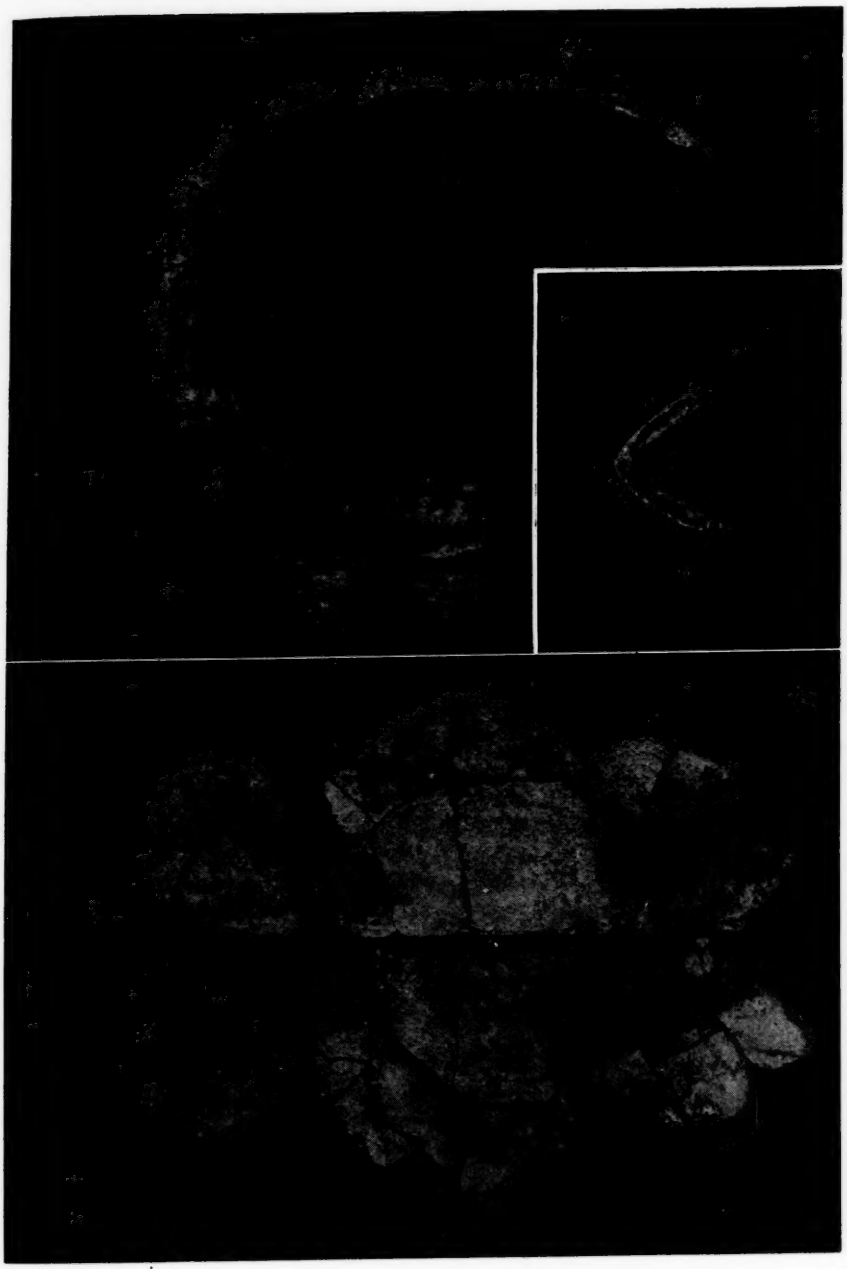
Text-fig. 1–6

Testudo turgida COPE, 1892, Am. Philos. Soc., Proc., vol. 30, p. 127.
Testudo riggsi HIBBARD, 1944, The Univ. Kansas Sci. Bull., vol. 30, no. 7, p. 71–76.
Gopherus turgida WILLIAMS, 1950, Am. Mus. Nat. Hist., Bull., vol. 95, art. 1, p. 1–36.

The type specimen of *Testudo turgida*, no. 14689, Acad. Nat. Sci. Philadelphia was found near Espuella, Dickens County, Texas in "Blanco beds" which are described as the same horizon as those of Crosby County. The specimen consists of a complete plastron with fragmentary left costals and right peripherals and additional vertebral plates. Originally described by Cope (1892) with measurements only and reprinted in Hay (1904) it is illustrated here for the first time (Text-fig. 1A, 1B).

W. F. Cummins found this turtle in 1891 3 miles N of Dockum, Dickens Co., Texas while making a survey of the "Staked Plains." At this time Cummins (1892) considered all post Dockum beds (post-Cretaceous) to be Blanco Canyon beds (now Blanco beds) and of Tertiary age. No specimens were found in Crosby County near Mount Blanco at this time. Cope in describing the specimen from Dickens County considered it Pliocene. Gidley (1903) showed the Blanco beds to be of more limited extent than indicated by Cummins but did not include in his account any description of the Dickens County locality. Gidley at that time considered the Blanco beds to be Pliocene. This specimen in all later listings has been included with the fauna from the Blanco beds of Crosby County.

Evans & Meade (1945) considered the deposits along the Blanco River to be basin fillings and while correlation between basin deposits could be made stratigraphically no connections were discernable. No mention is made of any Dickens County locality nor does the section given by Cummins correspond with any of the Blanco sections of Evans & Meade.



TEXT-FIG. 1—*Testudo turgida*. *A,B*, holotype, Acad. Sci. Philadelphia 14689, *A*, ventral view of plastron; *B*, dorsal view of carapace, ×¼. *C*, dorsal view of lower jaw, UMMP 31191, ×0.94.

Meade (1945) found more turtle material, however, does not say whether this material is *T. turgida* or not. None of the fauna which he described came from Dickens County sites.

Savage (1955) showed, on the basis of the stegomastodonts, that the Pliocene Rexroad fauna is older than the Blanco-Cita Canyon faunas. Since this turtle is well represented in the Upper Pliocene Rexroad fauna and older faunas of Kansas and Oklahoma it is probable that the Dickens County locality is also older than the Crosby County localities and may be of Pliocene age. If not this would be the first Pleistocene record of *Testudo turgida*.

This is a small turtle. The plastron measures 220 mm. in length which indicates that the turtle was approximately 150 mm. wide. The epiplastral lobes are bifurcate, conical and extremely robust. Each portion of the epiplastral plate forming these projections is cylindrical providing a rounded curvature both dorsally and ventrally. The suture between the two epiplastral plates is prominent. Each lobe terminates in a divergent conical projection. The anterior lobe behind the epiplastral lobes is massive becoming thinner at the posterior margin of the entoplastron. The remainder of the plastron is generally thick though not excessively so. The xiphiplastral notch is well developed. As noted by Cope the mid-longitudinal sulcus is extremely deep.

Certain proportions of the plastral scutes may have relation to its generic placement. The pectoral scute near the mid-line is 20 mm. long. The abdominal scute is 63 mm. long making the pectoral scute approximately $\frac{1}{3}$ the length of the abdominal.

The portions of the carapace present (Text-fig. 1B) show a well developed elongate and globose nuchal scute. The first vertebral scute is trapezoidal. The pleural plates show only slight alternate wedging. The anterior and posterior peripherals are massive and rounded. The free edges of the anterior curling upward.

In describing this turtle Cope pointed out the rugosities of the scutellation, the depth of the dermal scute lines and the general robust character of the turtle. In commenting on the portion of the carapace present he noted the annular growth ridges and their rugosities. He also noted the recessed areas of central growth of the scutes. The specimen at hand fits the measurements which he gave fairly accurately.

There are a group of sutured dermal ossicles of large size with the specimen (Text-fig. 4B). These are caudal plaques extremely developed and large in proportion to the size of the specimen.

A later report of Cope (1893) states that seven specimens were found together at one locality. These specimens, supposedly in the University of Texas Museum, could not be located.

Numerous specimens of this turtle have been collected in Pliocene localities in southwestern Kansas and northwestern Oklahoma. The following faunas have produced identifiable specimens.

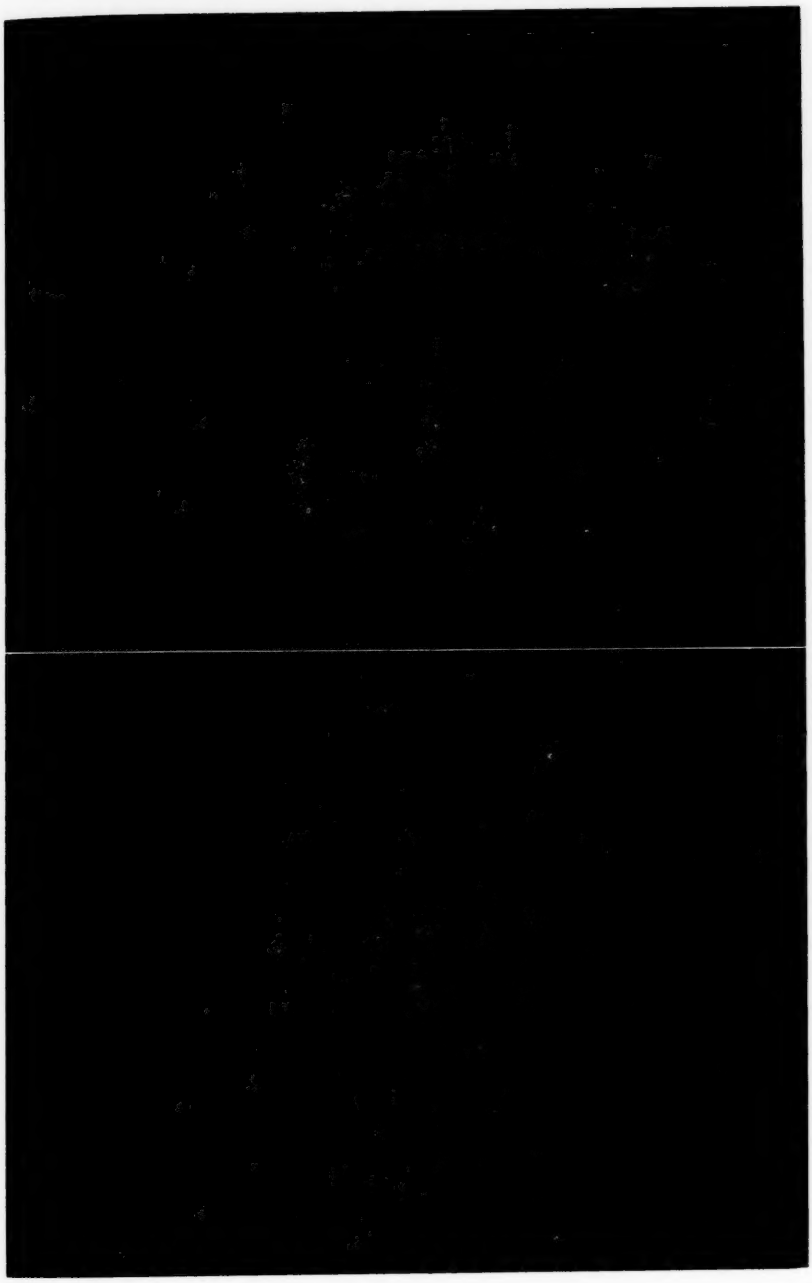
1. Saw Rock Canyon Fauna (Hibbard, 1949, 1952) XI Member of Rexroad formation, lower Upper Pliocene, latest Hemphillian or earliest Blancan.
2. Rexroad Fauna (Hibbard & Riggs 1949) Upper Pliocene, upper part of Rexroad formation, Blancan.
3. Buis Ranch Fauna (Hibbard, 1954) Ogallala formation, upper Middle Pliocene, late Hemphillian.

These faunas represent a time spread throughout the Middle and Upper Pliocene in Oklahoma and Kansas. These turtles have not as yet been found in Pleistocene deposits. The major portions of the material discussed here have come from the first two faunas. Because of the slight differences in the specimens from two localities, the material from each will be considered separately.

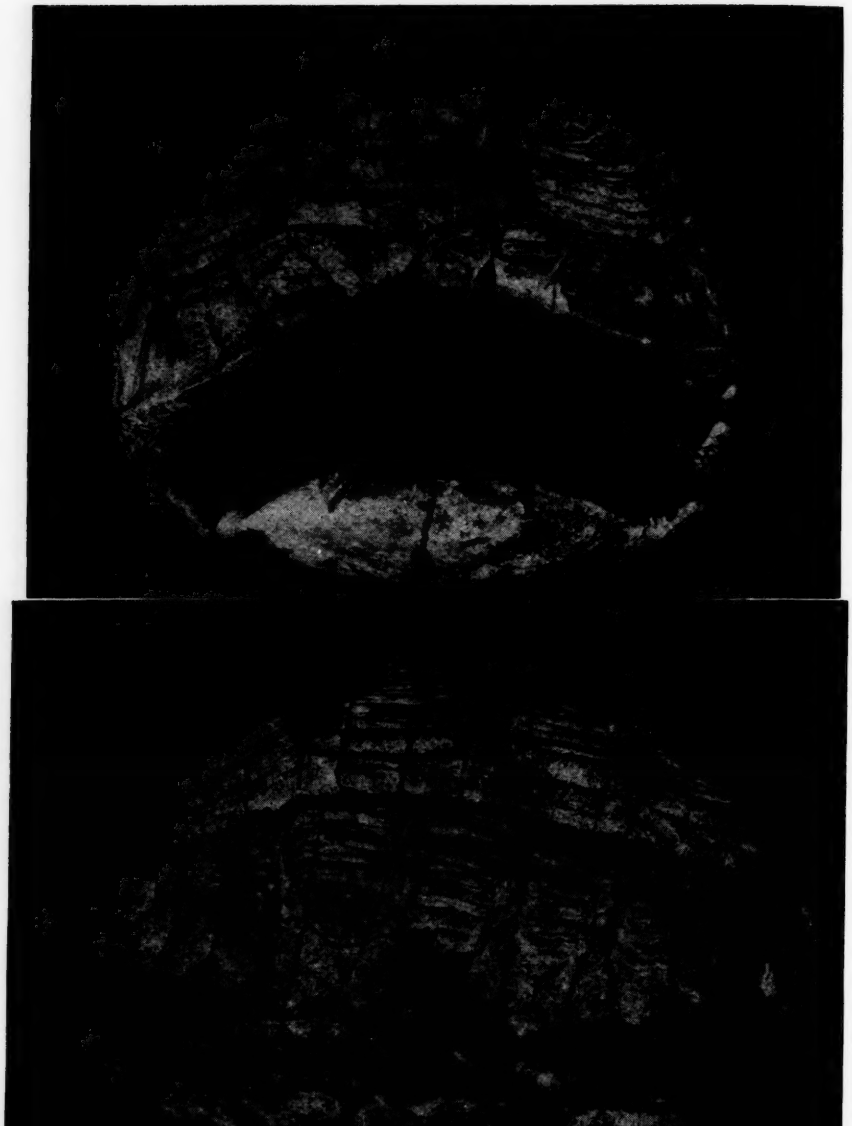
Locality 1.—Univ. Kansas locality 6, Seward Co., Kansas, Sec. 36, T. 34 S., R. 31 W., XI Ranch, S side of Cimarron River, Saw Rock Canyon Fauna.

Material from this locality is represented by the type, paratype and a fairly complete though disarticulated topotype, all of which were closely associated.

The type description (Hibbard, 1944) is entirely adequate although the discovery of additional specimens demands further description and more adequate illustrations. Photographs of the type specimen, KU 6789 (Univ. Kansas, Mus. Nat. Hist.), are presented here (Text-fig. 2,3) since they rep-



TEXT-FIG. 2—*Testudo turgida*. Carapace, KU 6789 (holotype of *T. riggsi* Hibbard). *A*, dorsal and, *B*, ventral view, $\times\frac{1}{4}$.



TEXT-FIG. 3—*Testudo turgida*. Complete shell, KU 6789 (holotype of *T. riggsi* Hibbard). *A*, anterior and, *B*, lateral view, ×½.

resent the most complete individual. Measurements can be found in the type description. These are point to point measurements and do not follow the curvature of the specimen.

In the type description and in the remarks of Williams (1950) resemblances to *Gopherus berlandieri* (Agassiz) have been noted. After examining the specimens as well as numerous *G. berlandieri* I find that the major similarity is that of size, and that the dissimilarities are more numerous and more

significant than this similarity. See discussion later.

It should be emphasized that *T. turgida* is an extremely high-arched turtle. The peripherals account for a major portion of the height since they are long and almost perpendicular throughout. The length of the lateral peripherals (4, 5, 6, and 7) averages 84% of the length of the associated costals (2, 3, 4, and 5). In *G. berlandieri* this is 71%. The high-arched carapace and its rounded surfaces, both anteroposteriorly and transversely, can be seen in the accompanying illustrations (Text-fig. 3A, 3B) as well as the outlines (Text-fig. 6).

A well developed gibbose nuchal scute is present, 10 mm. long and 7 mm. wide. The pygal bone is well indented from the margin of the peripherals. The costal plates do not show the distinct alternate wedging characteristic of many species of fossil and recent *Testudo* and *Gopherus*.

The vertebral scutes are characteristic. The first scute is extremely broad anteriorly, 57 mm., and narrows to 34 mm. as it joins the second vertebral scute. Vertebral scutes 2, 3, 4 have an average width (greatest) of 47 mm. This width is approximately 80% of the length of the costal scutes 2 and 3 (60 mm.) with which they interdigitate.

The anterior and posterior marginals though moderately massive are not disproportionately so. They are large globose and rounded and decrease to a fairly sharp edge at their free margin. The posterior ones are shorter and stubbier than the anterior.

In regard to the plastron, the gular projections of the epiplastron are conical, massive and extremely gibbosed almost to the point of being out of proportion to the rest of the turtle. This massiveness encompasses the entire anterior lobe of the plastron. It may be pointed out that the entoplastron is in contact with the pectoral scute and the pectoral scute is long. It measures 13 mm. along the mid-line, which would make it approximately a quarter the length of the abdominal scute which is 50 mm. long.

A general characteristic of the turtle occurring in all specimens is the gibbosity of all of the scutellations. The indentations between the scutes are extremely deep. The annular growth rings are prominent and the centers of growth are deeply recessed. The tendency to gibbosity is not only seen in the scutellation and gular projection of the epiplastron but in the projection of the peripherals of the carapace and to a lesser degree with the anal lobes of the xiphiplastron. The plates throughout are thick.

Associated with the type specimen are fragments of the internal skeleton. None of sufficient completeness to describe. There are, however, a group of well ossified sutured dermal ossicles each averaging $\frac{1}{4}''$ square and $\frac{1}{8}''$ thick.

Specimen KU 6790, the paratype, has a complete plastron and partial carapace. It is slightly larger than the type. A difference exists between this and the type in that the paratype shows a smoother and much less rugose surface both in scutellation and annular growth rings and in the degree of gibbosity. This pertains to all parts of the plastron and carapace. All other characteristics are essentially the same. Hibbard suggests that this might be a sex distinction. The pectoral scute is 15 mm. and the abdominal scute 55 mm. long. Associated with the paratype are a group of well developed sutured dermal ossicles similar to those found in the type.

Specimen UMMP 28452, a topotype, is a nearly complete disarticulated specimen. Though poorly preserved, this specimen has a partial skull, skeletal elements and shows that the feet and tail were covered with osseous dermal plates. The specimen is small, the plastron measuring 170 mm. in length. The epiplastral lobes are enlarged conical and gibbosed to a greater degree than the other specimens from this locality and resemble the epiplastral lobes of the turtles from the other locality (north side of the Cimarron river). The pectoral scute is one-fifth the length of the abdominal scute. The skull shows only the basisphenoid and basiooccipital areas and some of the frontal and parietal areas. In the carapace there is some indication of alternate wedging between the costal plates. The plates of this specimen are generally thicker than those of the other specimens from this locality.

Numerous disassociated bones from these turtles have been collected at this locality. They show a greater degree of gibbosity than the more complete specimens.

The three specimens from this locality present fairly consistent characteristics with the exception of the magnitude of gibbosity. The paratype is smooth, the type more rugose and in the additional topotype a greater degree of gibbosity. Isolated, associated plates show extremes in gibbosity as is found in other localities. This character seems diagnostic but at the same time its presence seems to be only a matter of degree.

Locality 2.—North side of the Cimarron Valley approximately 2½ miles from the type locality (apparently the same horizon) (Hibbard, 1949), located in Holmes pasture, SW ¼ Sec. 20, T. 34 S., R. 30 W., Meade Co., Kansas.

Three specimens have been collected from this locality by the University of Kansas field parties and one by the University of Michigan field parties. These specimens show some characteristics which appear to be peculiar to this particular assemblage as was mentioned by Williams (1950). The bony plates are of a greater thickness, the scutellations are marked by greater gibbosity and greater depth between scutes; however, the size and shape and other morphological characters of the specimens are essentially the same as those from the type locality in Seward County.

Specimen UMMP 31191 is the most complete of the specimens from the locality on the north side of the Cimarron river. It consists of the anterior half of the plastron, a nearly complete carapace, internal skeletal elements, an articulated series of dermal ossicles and a lower jaw.

The plastron (Text-fig. 4D) shows pronounced gibbosity in all scutellations especally with the epiplastral lobes. The pectoral scute is 7 mm. long and the abdominal scute is 52 mm. long.

The lateral peripherals (4, 5, and 6) are long and average 60 mm. in height. The costals (2, 3, 4, and 5) average 68 mm. in height. The peripherals, therefore, are 88% of the length of the costals.

The carapace (Text-fig. 4A) is somewhat warped and flattened. The free peripherals, both anterior and posterior, are gibbose and their margins are more rounded than those from locality 1. The plates are thick, the nuchal scute is rounded and elongate. The vertebral scutes are depressed or excavated along the mid-line. The average width of the vertebral scutes 2, 3, and 4 is 52 mm. The average length of the costal scutes 2 and 3 is 59 mm. making the vertebral scute 87% of the length of the costal scute.

The first vertebral scute is broader at its anterior margin than at its posterior margin making it trapezoidal in shape. The costal plates show some indication of alternate wedging. The pygal is well indented from the margin of the peripherals.

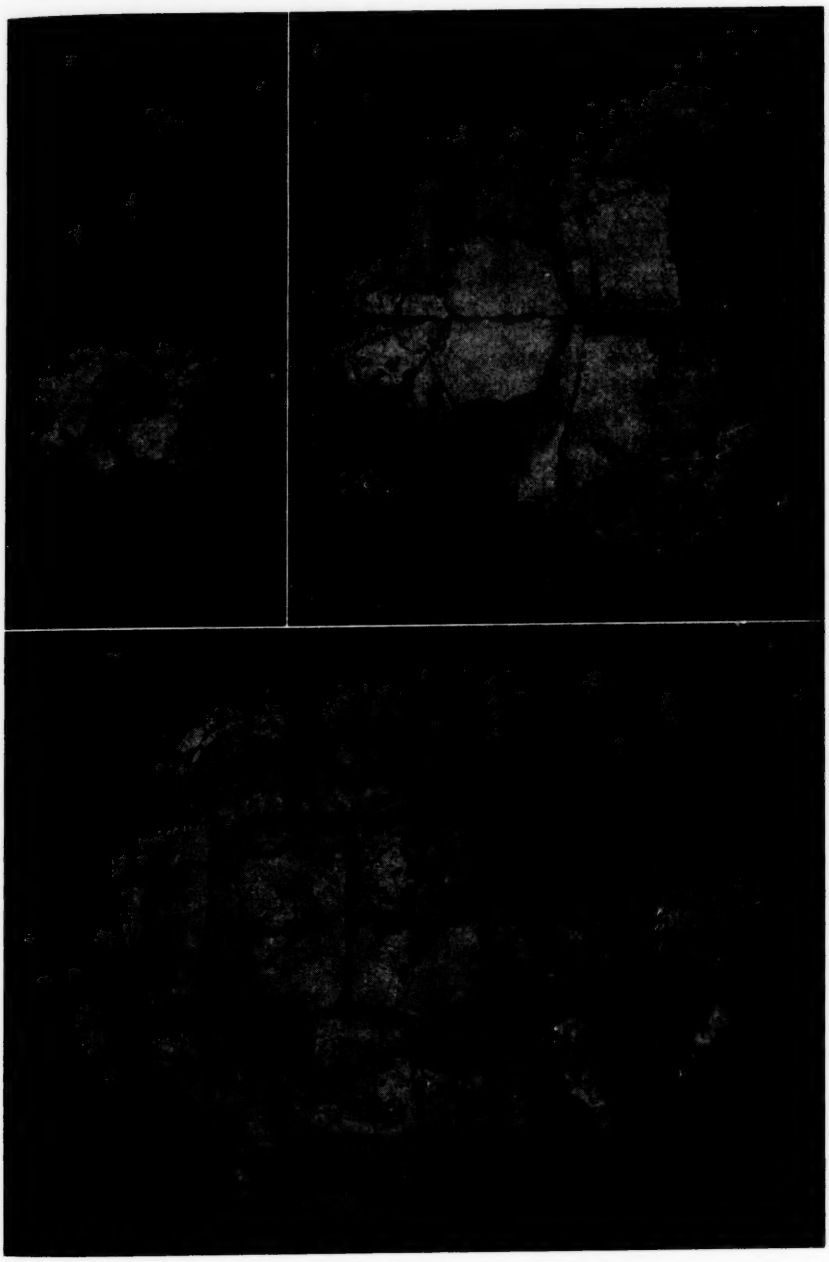
Though generally gibbose, throughout the annular growth rings are more prominent on one side than on the other.

Acetic acid preparation provided a complete osseous dermal caudal plate (Text-fig. 4C). The plate is well ossified and raised in the center into a crest. The individual ossified plates are a variety of shapes and sizes—rectangular, hexagonal or irregular.

In addition to some internal skeletal parts, a nearly complete lower jaw was found as well as an associated jaw of the same size. The jaw is complete (Text-fig. 4C) from the coronoid process forward consisting primarily of dentary, and shows two triturating ridges one inside and one out with a depression between. The depth is 8 mm. at the coronoid process and 5 mm. at the anterior end of the triturating ridges. The two rami join in the symphysis at the mid-line which is raised into a pointed process above the level of the triturating ridge. This elevates the symphysis to 7 mm. in height. The triturating ridges terminate 4 mm. from the symphysis. The length of the rami from the coronoid forward is 17 mm.

There is also an associated jaw identical in all respects with UMMP 31191, though only the symphysis is present. This, too, shows the raised and pointed symphysis.

Specimen KU 7404, is a complete plastron with portions of the marginals. Though complete the plastron is malformed, the bridge on the right is only three fourths of the length of that on the left. The mid-line also deviates slightly to the right. The total length of the plastron is 178 mm. The pectoral scute is 15 mm. in the mid-line or one third of the length of the abdominal. The other characters of the



TEXT-FIG. 4—*Testudo turgida*. *A*,*C*,*D*, UMMP 31191. *A*, dorsal view of carapace, ×½; *C*, sutured caudal plaque, ×¾; *D*, ventral view of plastron, ×½. *B*, Acad. Sci. Philadelphia 14689, sutured caudal plaque, ×¾.

plastron are the same as the other specimens from the same locality. In acid preparation osseous dermal and caudal plaques were found.

Specimen KU 7405, is an incomplete plastron showing only the pectoral and abdominal scutes. The pectoral is 17 mm. long while the abdominal scute is 47 mm.

Specimen KU 7406, is immature, though it is well-sutured throughout. The specimen consists of a partial carapace and a complete plastron. The plastron, 112 mm. long, generally shows the shape and characteristics of the adult, however it is proportionately broader. The gibbosity of the epiplastron and scutellations as well as the rugose annular growth rings are as in the adult. The completeness of this specimen and its general adult proportions indicate that the other specimens are undoubtedly adult. The pectoral scute is 7 mm. long, the abdominal one 35 mm. The entoplastron in this specimen as well as two other immature individuals is distinct in that it is elongate and longer than wide. This condition seems to reverse in the adult. Though small, osseous dermal plaques are present.

Locality 3.—NE ¼, SE ¼ Sec. 5, T. 5 N., R. 26 E.C.M., Beaver County, Oklahoma.

Five specimens have been collected by the field parties of the University of Michigan Museum of Paleontology in the Buis Ranch fauna (Hibbard, 1954).

Specimen UMMP 29151 consists of both epiplastral lobes and entoplastron. Somewhat smaller than the specimens from either of the other localities, it consists of massive gular projections and pronounced gibbose scutellations. The entoplastron is wider than long and the mid-line sulcus is deep.

Specimen, UMMP 30192, from NE ¼, SE ¼ Sec. 29, T. 6 N., R. 26 E.C.M., Beaver Co., Oklahoma consists of only fragmentary peripherals which show the gibbosity characteristic of *T. turgida.*

Specimen UMMP 32661, is an immature fragmentary specimen of the size and characteristics of KU 7406 described above. Even these immature specimens show the extreme robustness of the epiplastral lobes. This can be considered as characteristic of the species and not just due to advanced age.

In the summer of 1955 the field party of the University of Michigan, Museum of Paleontology, found two more specimens at the Buis Ranch locality. These specimens, UMMP 33482 and UMMP 33483, approximately the same size (Text-fig. 5A, 5B), were found closely associated. They have plastral lengths of approximately 145 mm. and a greatest width of 110 mm. Portions of the carapaces of both specimens are present but fragmentary. The pectoral scutes are approximately a quarter the length of the abdominals.

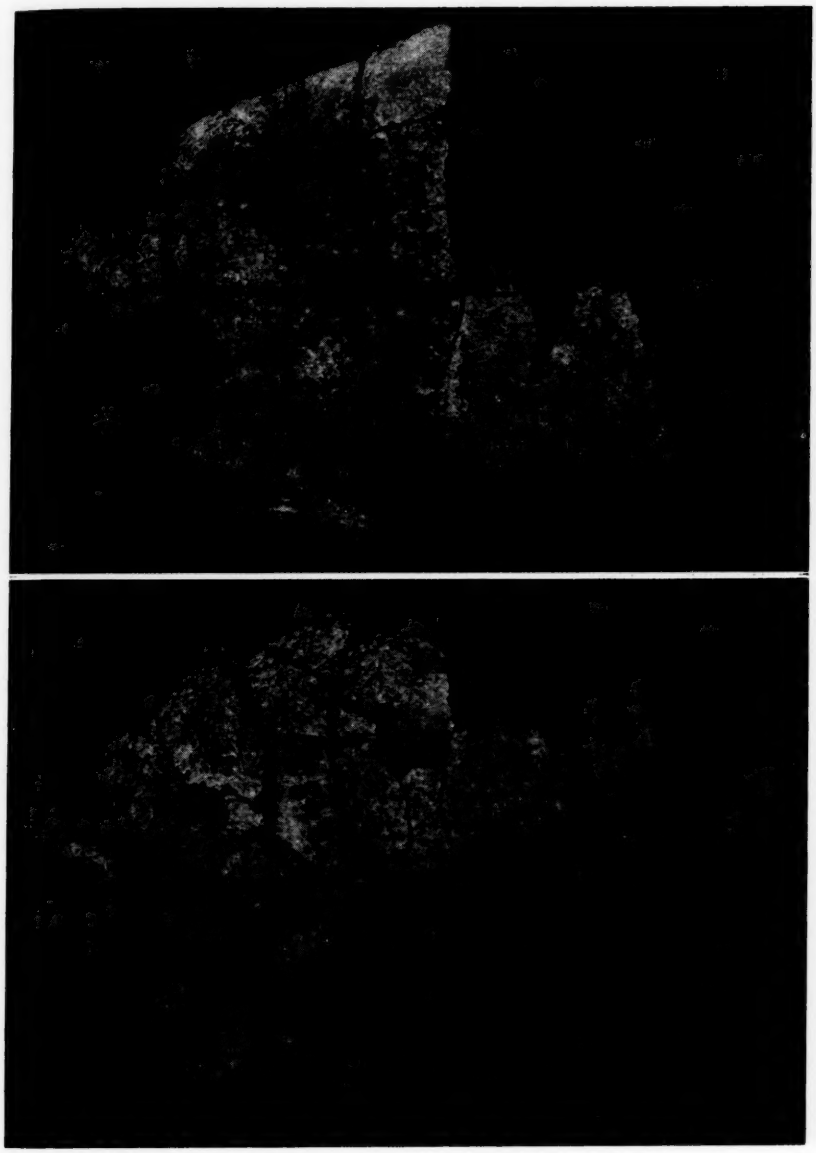
One of the specimens (UMMP No. 33482), shows the general characteristics of the turtles from the locality on the north side of the Cimarron River and the other (UMMP 33483) shows the characteristics of the turtles from the locality on the south side of the Cimarron (comparison of Text-fig. 1A and Text-fig. 4D with Text-fig. 5A will show the former similarity, whereas comparison of Text-fig. 2B with Text-fig. 5B will show the latter). Though these specimens are small they could not be considered immature. The differences in the two specimens at the Buis Ranch locality may be considered to be sexual but more significant, I think, is the similairity to the other turtles of similar age which had appeared different or thought to be distinct when found in separate localities.

All of the specimens from the Buis Ranch are small and not over 150 mm. in length. Whether this is indicative of the individual age of the specimens found thus far or due to their older geological age is not clear.

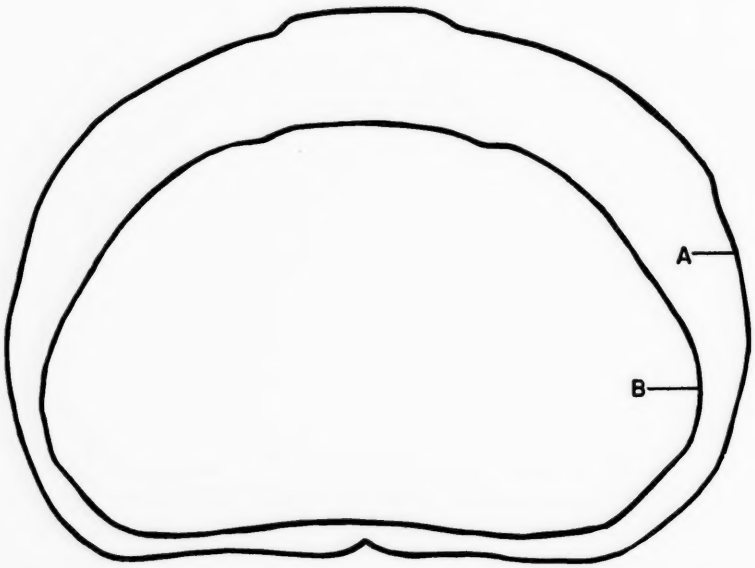
Specimen from Texas and Mongolia.—Two additional specimens which may be referred to the above turtles come from Texas. Both specimens are from the Panhandle Plains Historical Museum.

Specimen PPHM 1072, from Harrell Ranch bed no. 1, Axtel local fauna (Johnston & Savage, 1955) consists of small fragments of a turtle, an isolated entoplastron and a pygal bone.

Johnston also included a turtle from Cita Canyon, bed no. 2, (Lower Cita Canyon vertebrate assemblage) in his unpublished thesis, under the name of "*Testudo rugosa* sp. nov." (unpublished name), PPHM 1540. This turtle is small, 235 mm. long, plastron 212 mm. Because of its size and geologic age it may be considered by some equivalent



TEXT-FIG. 5—*Testudo turgida*. Ventral views of plastron, ×½. *A*, UMMP 33482; *B*, UMMP 33483.



TEXT-FIG. 6—Outline of cross section of shell. *A, Testudo turgida; B, Gopherus berlandieri.*

to the above turtles. The specimen consists of a complete plastron and carapace which is poorly preserved but which shows the annular growth rings so characteristic of the above turtles and also of immature turtles such as *Testudo rexroadensis* Oelrich, pieces of which are found in the Rexroad formation. The turtle shows no other characteristics of *T. turgida* and is in my opinion an immature specimen of the large turtles which are found in the Cita Canyon beds.

Testudo kalganensis Gilmore, 1931 (AMNH 6701) from the Cenozoic of Mongolia is a turtle similar in all morphologic respects to the specimens of *T. turgida* (see Williams, 1950). There is one character which distinguished this turtle and that is size. It is larger than any of the specimens described above. Gilmore estimated a length of 275 mm. which is a third longer than the specimens from North America.

Discussion.—The characteristics of *T. turgida* and *T. riggsi* are so similar that if one were unaware of the locality from which the specimens came the turtles would easily fit either description. Since they are approximately of the same age, same size and same characteristics I believe that they are synonymous.

As Williams pointed out, the specimens of *T. riggsi* from different localities do appear to have some differences. These differences are the degree of gibbosity of scutellation and the thickness of the plates. These differences disappear when one can find varying degrees within one locality as was found at the type locality. Furthermore, finding two associated specimens in the Buis Ranch fauna with characteristics of turtles from both of the other localities seems to indicate that the apparent differences in the described specimens of *T. riggsi* from southwestern Kansas were due to accidents of selective collection.

Direct comparison of Cope's type of *T. turgida* with the specimens from southwestern Kansas show no dissimilarities. In fact, the specimens from the north side of the Cimarron River (the more highly gibbose group) are almost identical in every detail. Because of this similarity it seems necessary to place the southwestern Kansas and the northwestern Oklahoma specimens of *T. riggsi* in synonymy with *T. turgida* as previously described by Cope.

Both turtles were originally described within the genus *Testudo.* Williams (1950) used a number of characters to differentiate Miocene *Hesperotestudo* from Miocene *Gopherus* and according, to their characteris-

tics, relegated thereto the variously described species of North American Cenozoic Testudinidae. Among these were *Testudo turgida* and *Testudo riggsi*, which were placed in the genus *Gopherus*.

Close examination of these specimens and comparison with Recent species of *Gopherus*, as well as the characteristics set up by Williams, fails to show any real relation to the genus *Gopherus*.

In the following discussion of the characters set up by Williams it is fully understood that his characters were intended to be indicative and tentative and not absolute. The characters will be given as pertaining to the genus *Testudo*.

1. "In the genus *Testudo* at the anterior end of the palate there is a premaxillary pit" as opposed to a median permaxillary ridge in the genus *Gopherus*. This character, though apparently minor, responds to the rule of either being present or absent. The palate of *T. turgida* is unknown; however, two mandibles described above show a distinctly elevated pointed process at the symphysis. Comparison of Recent mandibles of adult *Testudo* and *Gopherus* show that the *Gopherus* mandibles are notched at the symphysis to accomodate the premaxillary ridge while the mandibles of *Testudo* are pointed and elevated to fit into the premaxillary pit above. In some immature *Gopherus* the notching is not distinct. We are, however, dealing with an adult and with two specimens.

2. "External surface of dentary with fine vertical ribbing." The two specimens at hand show only the slightest signs of vertical ribbing and that is near the posterior end of the dentary. This character is inconclusive either way as far as those specimens are concerned.

3. Nuchal scute "much longer than wide." All of the available bones (9) contain nuchal scutes distinctly longer than wide and well gibbosed. In regard to the southwestern Kansas specimens (*G. riggsi*) the type and paratype do not show this as distinctly as other specimens from the same locality. The immature specimens show a tendency to be equivalent in width and length but only in two small ones.

In unprepared (with scutes on) specimens of *G. berlandieri* there may or may not be a nuchal scute; however, in all of the specimens I have examined in which the nuchal scutes have been removed there is no osseous representation of this scute. This variability of the nuchal scute was noted also by Williams in 1950. This is not only a characteristic of *Hesporotestudo* but it serves as a means of distinguishing *G. berlandieri* from *T. turgida*.

4. Shell shape, "tending to be high and globular." This character has been noted for the above described specimens. The globose condition undoubtedly caused the notation by both Hibbard and Williams of the resemblance to the Recent *G. berlandieri*. Text-fig. 6 illustrates the outline of both species graphically. The characteristic outline of *G. berlandieri* is the same for *G. polyphemus* (Daudin) and *G. agassizi* (Cooper). It may be noted that *Gopherus* is generally flattened dorsally but the dorsolateral and ventrolateral sides are flattened as well and each plane is separated from the other by a distinct angulation. This serves to distinguish the described specimens from *G. berlandieri* as well as to show the affinities of *T. turgida* to the genus *Testudo*.

5. Anterior shell margin "with flared anterolateral corners." This is probably a character of degree. There is distinct flaring in these specimens (see Text-fig. 2, 3) though not in all specimens.

6. Nuchal indentation "marked." Here again a matter of degree. In all of the specimens there is a marked nuchal indentation.

7. Fourth vertebral scute "as long as wide." In the specimens at hand the fourth vertebral scute is wider than long. This seems to be a gopheroid character, however I believe that this is a character of this particular turtle as a result of its truncation and globose nature, and in this character somewhat resembles *T. orthopygia* (Cope). In proportion to the other parts of the carapace the vertebral series is narrow.

8. Entoplastron "wider than long" of the eight entoplastra available five are wider than long, one as wide as long and the two immature specimens longer than wide. In all cases the differences are insignificant, however, it seems characteristic that progressively the older specimens have wider entoplastra.

9. Pectoral scute "In contact with entoplastron—1/15 to 1/30th abdominal scute." In all specimens the entoplastron is in contact with the pectoral scute. The proportional length between the pectoral scute and abdominal scute varies from 37% to 13% or from one-third to one-eighth. Williams later pointed out (1953) that this character alone is not necessarily indicative of an affinity to the genus *Gopherus* since *T. brontops* Marsh and *T. amphithorax* Cope showed a proportional length of from one-third to one-fifth.

10. Neural plate "fully differentiated second and fourth octagonal third and fifth quadrilateral." This is characteristic of all specimens of *G. turgida*, though I am not certain of its usefulness as a diagnostic character.

11. Dermal ossicles on fore and hind limbs and tail "present and extremely developed, often compact and suturally united." This is characteristic of all specimens. Osseous foot plaques are found in all specimens. A well developed caudal tail plaque in which the elements are suturally united is preserved in Cope's type of *T. turgida* as well as KU 7404 and UMMP 31191. Sutured tail plaques have been found with all specimens. For the comparatively small size of the turtle the dermal plaques are large and thus extremely prominent and well developed in this species.

In summing up the characters used by Williams to show affinities to the genus *Testudo*, it is obvious that of the 11 characters discussed 8 would be definitely considered to show affinities to the genus *Testudo*. Two characters are considered to be indeterminate, that of the proportions of the pectoral scute could fit either group and characteristic. The proportion of the third vertebral scute is possibly gopheroid. Two characters, the presence of the elevated mandibular symphysis and the presence of well formed osseous dermal plaques and caudal plates, seem almost conclusively characteristic of the genus *Testudo*.

Besides the characters discussed above, the following characteristics seem sufficiently diagnostic and consistent to use in separating the two genera.

In the genus *Gopherus* the vertebral scutes seem to be extremely broad, in contrast to narrow vertebral scutes in *Testudo*. A method of representing this is to contrast the width of vertebral scutes 2, 3 and 4 and compare their width to the average greatest length of costal scutes 2 and 3, with which they interdigitate. In the following tabulation percentages are used and are a comparison of the vertebral scute with costal scute.

Gopherus sp. (Pleistocene)		125%
G. polyphemus	(13)	111.5%
G. berlandieri	(10)	104 %
G. agassizi	(5)	97.7%
Testudo pardalis (Bell)	(5)	97 %
Testudo tabulata (Walbaum)	(7)	95 %
Testudo sp. Galapagos	(2)	86.5%
Testudo orthopygia	(2)	70 %
Testudo riggsi Ku 6789		80 %
Testudo riggsi UMMP 31191		88 %

From the above percentages it seems that with the genus *Gopherus* the vertebral scutes are as broad or broader than the length of the costal. The reverse seems to be the case in the genus *Testudo*. This character is subject to broad variability, as are the ones cited above.

The fossil specimens under discussion fall into the character percentage allocated to the genus *Testudo*.

As an almost direct corollary of the above character the first vertebral scute seems to have a distinct shape in the two genera. In *Gopherus* the first vertebral is generally square or its anterior margin is the same width as its posterior. In *Testudo* the posterior width is reduced making the shape of the first vertebral a trapezoid.

From a consideration of all of the above characters, it would seem that the above described turtles would fit best into the genus *Testudo*.

REFERENCES

COPE, E. D., 1892, A contribution to the vertebrate paleontology of Texas: Am. Philos. Soc., Proc., vol. 30, p. 127.

——, 1893, A preliminary report on the vertebrate paleontology of the Llano Estacado: Geol. Survey Texas, 4th Ann. Rept. (1892), p. 1–137, 23 pl.

CUMMINS, F. W., 1892, Report on the geography, topography, and geology of the Llano Estacada or Staked Plains: Geol. Survey Texas, 3rd Ann. Rept., 1891, p. 129–223.

EVANS, G. L., & MEADE, G. E., 1945, Quaternary of the Texas high plains: Univ. Texas Publ. 4401, p. 485–507.

GIDLEY, J. W., 1903, The fresh-water Tertiary of northwestern Texas: Am. Mus. Nat. Hist., Bull., vol. 19, art. 26, p. 617–635, 4 fig., 6 pl., 1 map.

GILMORE, CHARLES W., 1931, Fossil turtles of Mongolia: Am. Mus. Nat. Hist., Bull., vol. 59, p. 213–257, fig. 25–27, pl. 9.

HAY, O. P., 1904, Fossil turtles of North America: Carnegie Inst. publ. no. 75, p. 453.

HIBBARD, C. W., 1944, A new land tortoise, *Testudo riggsi*, from the Middle Pliocene of Seward County, Kansas: Univ. Kansas Sci. Bull., vol. 30, no. 7, p. 71–76, 2 fig.

——, 1949, Pliocene Saw Rock Canyon fauna in Kansas: Univ. Mich., Contrib. Mus. Paleont., vol. 7, no. 5, p. 91–105, 2 fig.

——, 1952, The Saw Rock Canyon Fauna and its stratigraphic significance: Mich. Acad. Science, Pap., vol. 38, p. 387–411, 5 fig.

——, 1954, A new Pliocene vertebrate fauna from Oklahoma: Mich. Acad. Science, Pap., vol. 39, p. 339–359, 5 fig.

——, & RIGGS, E. S., 1949, Upper Pliocene vertebrates from Keefe Canyon, Meade County, Kansas: Geol. Soc. Am. Bull., vol. 60, p. 829–860, 11 fig. 5 pl.

JOHNSTON, C., & SAVAGE, D. E., 1955, A survey of various late Cenozoic vertebrate faunas of the Panhandle of Texas, Part I: Univ. California, Publ. Geol. Sci., vol. 31, no. 2, p. 27–50, 5 fig.

MEADE, G. F., 1945, The Blanco fauna: Univ. Texas Publ. 4401, p. 509–556.

OELRICH, T. M., 1952, A new *Testudo* from the upper Pliocene of Kansas with additional notes on associated Rexroad mammals: Kansas Acad. Sci., Trans., vol. 5, p. 300–311, fig. 4.

SAVAGE, D. E., 1955, A survey of various Late Cenozoic vertebrate faunas of the Panhandle of Texas, Part II, Proboscidea: Univ. California, Publ. Geol. Sci., vol. 31, no. 3, p. 51–74, 8 fig., 2 pl.

WILLIAMS, E. E., 1950, *Testudo cubensis* and the evolution of the western hemisphere tortoises; Am. Mus. of Nat. Hist., Bull., vol. 95, p. 5–36, 8 pl.

——, 1953, A new fossil tortoise from the Thomas Farm Miocene of Florida: Mus. Comp. Zool., Harvard College, Bull., vol. 107, no. 2, p. 537–554, 1 fig., 4 pl.

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A CLASSIFICATION OF ECHINOIDS[1]

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ABSTRACT—The classification of class Echinoidea used by Mortensen (1928–52) is critically reviewed and revised. Two subclasses are recognized, of which one, the Perischoechinoidea, includes all the Paleozoic echinoids and the post-Paleozoic cidaroids. The remaining echinoids are placed in the subclass Euechinoidea. This is divided into four superorders, as follows:—Diadematacea (for the order Aulodonta as used by Mortensen plus the families Echinothuriidae and Pygasteridae); Echinacea (for Mortensen's orders Stirodonta and Camarodonta); Gnathostomata (for Mortensen's Holectypoida excluding the Pygasteridae, plus his Clypeasteroida and certain genera of his Cassiduloida); and Atelostomata (for the remainder of Mortensen's Cassiduloida and his Spatangoida). There is also some rearrangement on the ordinal level, but the families are left for the most part as used by Mortensen.

INTRODUCTION

NEARLY four years have elapsed since the completion of Mortensen's Monograph of the Echinoidea (1928–52) and it is now possible to see in perspective some of the effects of this monumental achievement on the course of research, at least from the paleontological point of view. The present authors consider that their conclusions, though far-reaching, are the natural outcome of a critical review of the Monograph in the light of their own investigations. They wish also to offer for criticism the classification which it is intended to use in the "Treatise on Invertebrate Paleontology."

We wish first to offer our gratitude and homage to the memory of Mortensen. His long and fruitful career spanned the interval between the ancien régime of Alexander Agassiz and the present generation. The world is not likely to see again so comprehensive a grasp of the whole subject nor such a massive body of wide and deep researches in any one man. Paleontologists have as yet only begun to see the great possibilities that Mortensen's methods of study have put before them.

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[1] Published with the permission of the Director, Geological Survey of Great Britain.

THE EARLIEST ECHINOID

The position of Bothriocidaris.—Mortensen finally concluded (IV, 1, p. 1)[2] that *Bothriocidaris* is not a true echinoid and that it has no genetic connection with the class. He sought an ancestor among the group of many-plated forms that includes *Myriastiches* Sollas and *Aulechinus* Bather & Spencer. It is to be regretted that *Bothriocidaris* was once so emphatically held to be the ancestral echinoid, since that attitude of mind led to the inference that an ancestor could be demonstrated. Yet, since in no other class of animals is a generic form claimed as aboriginal per se, it is unlikely that the echinoids should be specially favored by the geological record.

Whatever weight may ultimately be allowed to the arguments adduced from the ontogeny of Recent forms, it may be worth while to consider three pieces of direct evidence as to the affinities of

[2] For the sake of convenience, all references to the Monograph of the Echinoidea are given by volume and page number only. Other references are given by author, date and page in the usual manner.

Bothriocidaris. First, it possesses typical echinoid tube-feet (II, p. 8) whose anatomical relationships are more like those seen in later echinoids than in any other class of echinoderms. If this is a case of convergence or parallelism, it is a striking one to be displayed at such an apparently early stage in the history of the phylum. Secondly, the primordial ambulacral plates [Mortensen showed that the "teeth" of earlier authors are plates, but in accord with Hawkins (1929) we consider that they might be peristomial plates] are arranged according to Lovén's law (Jackson, 1912, p. 241). Now it is obvious that in any structure composed of two alternating columns of plates, one primordial plate must be larger and the other smaller. Given five ambulacra so constructed, there are theoretically $2^5=32$ possible patterns and a particular pattern would be expected to occur in about 3 per cent of cases. Yet in all echinoids where their arrangement has been studied (except in certain clypeasteroids) the primordial ambulacral plates are arranged in the same way. Lovén (1874) has demonstrated the origin of this arrangement in the symmetry of the larval echinoid. While it cannot be stated that the disposition of these plates in the same way in *Bothriocidaris* is an effect of the same cause, it is surely no mere coincidence. Thirdly, in its five well-defined ocular plates, the apical system of *Bothriocidaris* is nearer the condition typical of later echinoids than that of any other echinoderm and in fact than that of any of the earliest Lepidocentridae. When the ontogenetic arguments are added (Hawkins, 1931) it may fairly be conceded that *Bothriocidaris*, ancestral or not, is a true echinoid.

If this be accepted, it is then necessary to imagine an ancestral form from which both *Bothriocidaris* and the earliest Lepidocentridae could have descended. It does not follow that either is in the direct line of descent from the hypothetical ancestor to the known later forms. What must be borne in mind is that the evolutionary potentialities capable of producing both bothriocidaroid and lepidocentroid types were present in the unknown ancestral stock. It has then to be explained how the characters that have been held to indicate a connection between *Bothriocidaris* and post-Paleozoic echinoids are not seen in the Lepidocentridae and yet appear in their archaeocidarid and further derivatives.

Myriastiches was held by Mortensen (II, p. 56; III, 1, p. 349) to be the oldest known echinoid. It was the opinion of P. Lake that raphiophorid trilobites associated with the holotype (and only known specimen) indicated a Middle Ordovician (Llandeilian) age: *Bothriocidaris* is from Upper Ordovician (approximately Caradocian) strata of Estonia, while *Aulechinus* and its associates occur in still higher Ordovician (Ashgillian) beds at Girvan, Scotland. It is now, however, practically certain that *Myriastiches* is not so old as had been thought. It is unfortunate that the locality of the holotype is not known, but in the opinion of Dr. C. J. Stubblefield the trilobites, whose association with the echinoid is unequivocal, resemble Silurian raphiophorids more closely than Ordovician members of the same family. Photographs of these specimens and of *"Ampyx" rouaulti* Barrande from the Silurian, Ee_1, of Borek, Bohemia and of two British Silurian raphiophorids were sent to Professor H. B. Whittington, who reported:

> Photographs of these tiny trilobites were sent to me, and there is no doubt that they are raphiophorids. The cephalon is typical, the glabella narrow near the base, and small alae seem to be present. The thorax seems to consist of five segments, the anterior markedly longer than those succeeding. There is a suggestion of small anterolateral lobes on the axial rings, and the pleural furrow on the first segment is at first directed strongly backward and outward, then curves outward and distally forward. Its course thus has a pronounced curve, concave forward, and the pleural furrows of the second and third segments have a similar but less pronounced curve. The small pygidium shows three pairs of pleural furrows, also having a faint curvature concave forwards.
>
> The thorax and pygidium, as well as the cephalon, of *Raphiophorus rouaulti* (Barrande) and of the British Wenlock species are remarkably similar, and show the characteristic lobes on the axial rings of the thorax, long first segment and peculiar curve of the pleural furrows. A longer first segment is a common character in raphiophorids, but in Ordovician forms such as *Ampyx*, *Edmundsonia* and *Lonchodomas* the pleural furrow runs in a curve gently convex forwards. In such Ordovician genera as *Ampyxina*, *Raymondella* and *Anisonotella* the

same curve is quite strongly convex forwards. It seems that only in the Upper Ordovician and Silurian species at present placed in *Raphiophorus* is there a curve concave forwards, a curve which is marked in Wenlock species.

I conclude that the probability of the raphiophorid associated with *Myriastiches* being of Silurian age is strong. I know of no Ordovician raphiophorid species with which it can be at all closely compared, but the likeness of the thorax to that of British and Bohemian Wenlock forms is striking.

There is also a considerable fragment of a graptoloid stipe associated with the echinoid. According to Professor O. M. B. Bulman this is indeterminable, possibly a monograptid or dichograptid. If the latter, however, it is most like a rare species of Llanvirnian age, so that there would be discrepancy with the trilobite evidence even if these were Ordovician. A fragment of a phyllocarid crustacean is also present, but this has not yet been determined.

The open radial groove said by Mortensen (II, p. 56; III, 1, p. 349) to be present in *Myriastiches* does not exist. The specimen is for the most part an internal mold, so that the structure interpreted as an external groove is in fact the mold of a convex structure on the interior surface of the test. The morphological characters of *Myriastiches* are in fact very like those of the Silurian *Echinocystites;* there is nothing visible to contradict the evidence in favor of a Silurian age provided by the associated fossils. The claim that *Myriastiches* must be nearer the root stock of the Echinoidea because it is geologically older than *Bothriocidaris* has no longer any validity.

PALEOZOIC ECHINOIDS

Among the bothriocidaroid characters to be expected in descendants of a stock to which *Bothriocidaris* is related there would certainly be the presence of a single plate at the adoral termination of each interambulacrum. Mortensen (II, p. 17) attributed this condition to the mechanical requirements of space, but this does not explain why the ambulacra, however sharply constricted adorally, always end in a pair of plates; nor why the primordial interambulacral plate may be larger than, or at least as large as, the pair in the succeeding row in young echinoids (and often also in adults); nor why the interambulacra usually end in two columns adapically in a space often more confined than that available adorally. It may be tentatively suggested that in forms without a perignathic girdle (e.g., Echinocystitidae = Lepidocentridae), a single primordial interambulacral plate provided a firmer anchorage for the muscles of the lantern than would two smaller plates. Attention may also be drawn to the single-columned interambulacra of *Cravenechinus* Hawkins.

A second bothriocidaroid character which would be expected in Echinocystitidae, if some such characters are assumed to have been present in their ancestor, is the Lovénian arrangement of their primordial ambulacral plates. Unfortunately, even in well-preserved specimens, it is a matter of great difficulty to trace the boundary between the plates of the corona and those of the peristomial membrane and thus almost impossible to identify the row in which the Lovénian formula might, or might not, be discerned.

The parallel between Paleozoic and Mesozoic echinoids in ambulacral evolution has been discussed by Hawkins (1943). In both there is expansion of the water-vascular system expressed by increase in the numbers of tube-feet. In the Echinocystitidae these were emplaced in large numbers of small, independent, imbricating ambulacral plates. The intervening spaces were filled by many small, thin, imbricating interambulacral plates, the whole flexible structure being mechanically weak. Gradually the corona came to be built on a stronger pattern; and while the water-vascular system was still served by many small plates, the interambulacra came to be constructed of fewer, larger plates, rigidly united to each other and each capable of supporting a single large radiole.

An attempt at such a massive test was made by the Palaechinidae, but the effort was short-lived. Within the space of Lower Carboniferous time they had advanced from the relatively simple *Palaechinus* to the peculiarly specialized *Maccoya* and *Melonechinus* and had passed away without known descendants. During the Lower Paleozoic two evolutionary courses were being followed among the Echinocystitidae (= Lepidocentridae). One led, by acceleration of "lepidocentrid" characters, to large, scaly,

flexible forms such as *Hyattechinus* and *Meekechinus*. The other led to the Archaeocidaridae and through them to the Cidaridae and later groups of echinoids.

It was in this second trend that the bothriocidaroid characters were combined with new features to give the echinoids the freedom of the Mesozoic seas. The number of ambulacral columns was fixed at two, as indeed it had always been in many Echinocystitidae. The interambulacral columns were also limited in number to two. Now since each interambulacrum had always started with a single plate, and since new columns had been introduced more or less gradually in the ontogeny, this need only have been a matter of retardation of the development of interambulacral columns. From the numerical standpoint, the two-columned interambulacrum of *Miocidaris* or any cidarid is a permanently fixed young stage of a "lepidocentrid" such as *Lepidocidaris* with six to eight columns in the adult. The evolutionary dichotomy between the specialized Echinocystitidae and the archaeocidarid stock is thus conceived as a difference between recapitulation and acceleration in the former and paedomorphosis and retardation in the latter.

POST-PALEOZOIC ECHINOIDS

By the end of the Permian all the echinocystitoid echinoids had become extinct, leaving only the cidaroid lineage to continue into the Mesozoic and give rise to the highly diverse post-Triassic echinoids. Despite the fact that only a single genus (*Miocidaris*) is known to cross the Paleozoic-Mesozoic boundary, seven new regular (Pedinidae, Diadematidae?, Hemicidaridae, Acrosaleniidae, Pseudodiadematidae, Phymosomatidae, and Stomechinidae) and four irregular (Pygasteridae, Holectypidae, Galeropygidae, and Collyritidae) families had appeared by Domerian (Lower Jurassic) time. Of these eleven families none are known at present from beds older than Carnian (Upper Triassic). Among the irregulars, *Plesiechinus* of the Pygasteridae appears in the Charmouthian (*P. reynesi* Desor), *Holectypus* of the Holectypidae in the Domerian (*H. hians* Lambert and an undescribed British form), *Loriolella* and *Galeropygus* of the Galeropygidae also in the Domerian and *Pygomalus* of the Collyritidae in the Sinemurian (*P. prior* Desor). These genera thus apparently represent the roots of all the later irregular echinoids, and their relationships to one another and to the regular echinoids are of critical importance.

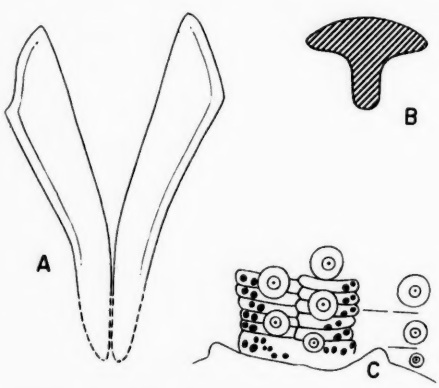
Despite the first occurrence of *Pygomalus* earlier than the first known *Galeropygus*, Beurlen (1934, p. 159) believed that the Collyritidae are descended from some hitherto undiscovered galeropygid ancestor, partly on the grounds that the periproct is further removed from the apical system in *Pygomalus* than in *Galeropygus*. *Galeropygus* itself has already evolved considerably from any possible regular ancestor. The test is thin, the radioles are small, closely set and of primary and miliary sizes only. The tubercles are perforate and crenulate and without any discernible orderly arrangement. The peristome is small and a little anterior in position and the apical system is central. The posterior genital plate appears to be absent, but in well-preserved specimens distinct articular surfaces can be seen, indicating the presence of one or more plates between the posterior oculars. So-called complementary or catenal plates are known in this position in the presumed derivative genera *Desorella*, *Menopygus*, *Hyboclypus* and *Infraclypeus*, so that the existence of similar plates in *Galeropygus* may be assumed even though their nature is unknown. The periproct is in contact with the apical system and is situated at the head of a deep, narrow sulcus extending to the posterior ambital margin. The ambulacra are very narrow and are separated into a trivium of three, nearly symmetrically-disposed, anterior areas and a bivium of the two posterior areas, which diverge from each other at an acute angle adapically and curve outwards towards the ambitus. There is a hypophyllode in which reduced plates occur and in which the pore-pairs are arranged in arcs of three.

There are no traces of a lantern or girdle in *Galeropygus*. Lambert & Thiéry (1914, pl. 8, fig. 8) illustrate an internal mold of *Desorella elata* showing what they consider to be imprints of auricles, but these structures are very small and seem to be situated on the margins of the interambulacra. Mortensen (IV, 1, p. 104) suggested that they

might represent branchial slits, but he overlooked the fact that they are impressions in an internal mold and must therefore represent raised structures on the inner surface of the corona. The figure is unfortunately too poor for any interpretation to be offered until more material has been examined. The living *Apatopygus recens* (Milne Edwards), here held to be descended from the galeropygid stock, has a well-developed lantern with keeled teeth in the early stages of growth, but no trace of lantern or girdle in the adult. These structures may thus have been developed in *Galeropygus* but lost in an early ontogenetic stage.

Loriolella Fucini is placed in the Galeropygidae by Mortensen (IV, 1, p. 106) and was considered ancestral to *Galeropygus* (Hawkins, 1922, p. 221). It is similar to *Galeropygus* in general shape, in the small peristome and narrow ambulacra and, superficially, in the tuberculation. There is a prominent swelling, which may represent a large primary tubercle, near the adradial margin of each adoral interambulacral plate. The periproct is in a shallow depression rather than a deep groove and there are distinct traces of branchial slits. *Loriolella* and *Galeropygus* may be collateral descendants of some irregular ancestor rather than directly linked genetically. *Pygomalus* is still the earliest known irregular echinoid and can only be linked with the Galeropygidae by postulating some unknown common irregular ancestor which in turn would have been derived from some stirodont regular form.

Plesiechinus and *Holectypus*, the only other known Liassic irregular echinoids, differ considerably from *Pygomalus* and *Galeropygus*. In both the peristome is much larger, central in position and provided with well-developed branchial slits. The ornament includes primary and secondary tubercles and miliary granules. The secondary tubercles form regular horizontal and meridional series at and below the ambitus and the ornament never has the crowded, disorderly appearance seen in *Galeropygus*. The ambulacra are relatively wider. The two genera differ from each other, however, in important features. The periproct is much more advanced in position in *Holectypus*. The tubercles are perforate and crenulate in *Holectypus* and the teeth are keeled (Text-fig. 1B). The tubercles are perforate and smooth in *Plesiechinus* and, although the teeth are unknown, the general resemblance to such Pedinid genera as *Palaeopedina* and *Hemipedina* suggests that they must have been grooved; the Bajocian *H. bonei* Wright, transferred to *Palaeopedina* by Lambert & Thiéry (1910, p. 196) can be shown by a study of growth-series to be a young form of *Plesiechinus ornatus* (J. Buckman). The radioles of *Holectypus* have a hollow axis (IV. 1, p. 27); those of *Plesiechinus* are not known with certainty, but several found adhering to the corona and within the peristome of a specimen of *P. ornatus* (British Museum [Natural History], no. E. 12081) have a solid axis, like the radioles of pedinids. In spite of earlier opinions that *Holectypus* was of pygasterid derivation (Lambert, 1900; Lambert & Thiéry, 1914, p. 277; Hawkins, 1920, p. 453, text-fig. 2; 1943, p. 69), it seems that the two must in fact be of independent origin (Mortensen, IV, 1, p. 14). *Holectypus*, in fact, shows many resemblances to the Pseudodiadematidae. In both the teeth are keeled and the tubercles perforate and crenulate, and the radioles lack a solid axis (in *Pseudodiadema pseudodiadema* the axis is filled with an irregular mesh work). The radial alignment of granules



TEXT-FIG. *1A,1B—Holectypus depressus* (Leske). British Mus. (Nat. Hist.), Dept. Geol., hypotype no. 34472. *A*, pyramid, ×9. *B*, *cross-section* of tooth, ca. ×20.

TEXT-FIG. *1C—Orthopsis granularis* (Agassiz & Desor). Hypotype, British Mus. (Nat. Hist.), Dept. Geol. base of ambulacrum V, ×4.5; plates obscure on peristomial margin.

from the primary interambulacral tubercles seen in the Pseudodiadematidae is paralleled by similar radial alignment in *Holectypus*. Backward elongation of the periproct in such a pseudodiadematid as *Heterodiadema* may represent a convergent tendency to an irregular condition.

In later holectypoids (*Discoidea*, *Conulus*) the tubercles are perforate and crenulate and the teeth are keeled. Similarly, perforate crenulate tubercles are the rule in most other groups of irregular echinoids. On the evidence summarized above, therefore, it seems most likely that the Pygasteridae are a sterile offshoot of the Pedinidae and that the Holectypidae are the ancestral family of the remaining Holectypoida (including *Echinoneus* although this has no lantern in the adult) and are perhaps near the root of certain other irregular stocks as well.

In summary of the preceding, it appears to us, as has already been hinted at by Hawkins (1912, p. 489; 1920, p. 456; 1943, p. 69) and Mortensen (IV, 1, p. 1), that the subclass Irregularia, as interpreted by Mortensen (IV, 1, p. 7) is polyphyletic and thus needs to be abandoned. We assume that the first regular echinoids to be differentiated from the cidaroid parent stock were aulodont forms and that the earliest stirodont forms were in turn derived from these; also that, except for the Pygasteridae, all the irregular echinoids originated from stirodont regular ancestors. The former assumption, which implies belief in a common cidaroid ancestor for both aulodont and stirodont regulars, is supported by the fact that both derivative groups possess a perignathic girdle, compound ambulacral plates, branchial slits, sphaeridia, and ophicephalous pedicellaria, and by the argument that the stirodont forms differ more widely from the cidaroid ancestor than do the aulodont. There is at present no evidence to show whether all the stirodont regulars descended from a single or from several aulodont stocks; it seems likely, however, that the irregular groups Gnathostomata and Atelostomata (see below) originated in distinct, though at present unidentified, stirodont roots.

By the end of the Mesozoic all the orders here recognized, except the Echinoida, had appeared. The cassiduloids and spatangoids are recognizable at the beginning of the Cretaceous, the temnopleuroids appear in the Lower Cretaceous, while the Echinoida are not reported earlier than the Eocene.

THE CLASSIFICATION OF THE ECHINOIDEA

General.—In 1935 (II, p. 4), Mortensen divided the Echinoidea into two subclasses, Pseudochinoidea (including only *Bothriocidaris*) and Echinoidea Vera. Later (IV, 1, p. 4) he reverted to the older division into Regularia and Irregularia and regarded *Bothriocidaris* as a diploporite cystoid. As indicated above, we prefer to regard *Bothriocidaris* as a true echinoid.

The subclasses Regularia and Irregularia under which Mortensen eventually grouped all the Echinoidea date as concepts from Cuvier (1817) and were especially familiarized by the work of Jackson (1912). Yet on several occasions and in several ways Mortensen indicated his belief that these groups did not correspond with natural phylogenetic lineages. Within the Regularia, for example, he derived some Aulodonta from lepidocentroid and others from cidarid ancestors, and associated some Camarodonta (the Orthopsidae) with an aulodont and others with a stirodont origin. He also suspected that the Irregularia were polyphyletically descended from Regularia. Attention may be drawn to the backward prolongation of the apical system in some Pseudodiadematidae and Phymosomatidae as showing a tendency in distinct, though related, lineages towards an irregular condition. His classification therefore fell short in obvious respects from the ideal degree of correspondence with assumed phylogeny. It is a principal aim of the present work to use the implications of his results, expanded and sometimes adjusted by our own evidence, in working out "a classification that shall reflect the major natural subdivisions" of the Echinoidea and "the main relationships indicated by current evolutionary theory" (Arkell, 1951, p. 355). In what follows we are assuming that all the regular echinoids (including the Echinothuriidae) are descended from cidarid ancestors and that all irregular echinoids are descended from regular echinoids of one kind or another.

The migration of the periproct took place

later in geological time and in evolutionary development than a series of other changes in echinoid morphology, thus it seems to us that the "regular" or "irregular" position of the periproct is not a sound character on which to base the primary division of the class. These earlier changes were more profound because the morphological conditions in which they are expressed are seen not only in irregular echinoids but also in all the post-Paleozoic regular echinoids except the Cidaroida. They are, in fact, the changes which differentiate these regular forms (Aulodonta, Stirodonta, and Camarodonta of Jackson and of Mortensen) from the Cidaroida and they are discussed in detail below. We regard it as logically necessary to attribute greater importance to the characters differentiating the regular echinoids from the Cidaroida than to those differentiating the regulars from their irregular descendants, even though not all the characters of the former category appear in all irregular echinoids. In general terms, if two groups, A and B, can be separated on named morphological characters, then the presumed descendants of B must be treated as still more distinct from A, whether all the characters used to differentiate A and B are seen in them or not.

No perignathic girdle is present in the Echinocystitidae, Palaechinidae or Archaeocidaridae. It is first seen in Permian species of *Miocidaris* where, as in all later Cidaroida, it consists only of interambulacral apophyses. In all other regular echinoids it consists principally of auricles, ambulacral in position and always larger than the apophyses. This pattern of girdle is also seen in the Pygasteridae and Holectypidae, but in the later Holectypoida and in the Clypeasteroida, the Conoclypidae and certain genera referred by Mortensen to the Cassidulidae, the apophyses are much reduced and the auricles have assumed an interambulacral position. In the remaining irregular groups the girdle has disappeared, at least in the adult stages. Thus it seems to us that the condition of the perignathic girdle is the most important of the characters in which the Cidaroida differ from the other regular echinoids.

Within the scope of the Cidaroida (including the Archaeocidaridae) there is thus a passage from the earlier, girdle-less condition to the first stage in the development fo the girdle. This takes place in late Upper Paleozoic time and the condition then attained has persisted unchanged in the Cidaroida until the present day. No Paleozoic echinoid or cidaroid possesses a complete girdle. This first appears in the aulodont (Triassic to Recent) and stirodont (lower Lias to Recent) regular forms. The morphological division between echinoids with and echinoids without a complete girdle therefore coincides approximately with the division between Paleozoic and later time; and (in spite of Mortensen's contrary views) no form with a complete girdle can, in the present state of knowledge, be traced to a Paleozoic ancestor, except through some Mesozoic cidaroid intermediary.

Next, all echinoids possessing a complete perignathic girdle also possess compound ambulacral plates (or are descended from such). These have been defined (Hawkins, 1920, p. 398, 387) as

> association of . . . [ambulacral] plates which are usually, and always primitively, grouped around, and bound together by, one or more large tubercles. . . . The plates become massed together into varying groups; the amount of sutural tissue between the components of a group is much reduced; and the welded plates are bound together by the extension over their surfaces of the closely-knit stereom of one or more large tubercles.

Nothing resembling this condition is seen in any Paleozoic echinoid nor in any cidaroid. Such ambulacral irregularity as is seen in them, however parallel in biological effect, is quite different in nature; and none of the included plates of an echinocystitid is morphogenetically comparable with a reduced plate of a compound ambulacral.

Thirdly, all the echinoids possessing a complete perignathic girdle and compound ambulacral plates possess also branchial slits, sphaeridia and ophicephalous pedicellariae. None of these are known in Paleozoic echinoids or in the Cidaroida.

The Cidaroida are in addition separated from the other post-Paleozoic regulars (and therefore from their presumed descendants) by the structure of the peristome. In the Cidaroida this is covered by many small ambulacral and non-ambulacral plates; in the others (except in adult Echinothuriidae) by only ten large ambulacral (buccal) plates and small non-ambulacrals. Other differ-

ences are less easy to define, but since these forms are held to be descended from the Cidaroida, their separation from the latter is inevitably to some extent arbitrary. The Cidaroida, however, retain in stable condition many primitive features of Paleozoic aspect and origin, so that it seems more logical to group them with the Paleozoic forms in a subclass, characterized by the lack of a girdle, compound ambulacral plates, sphaeridia, and ophicephalous pedicellaria, for which the name Perischoechinoidea McCoy is here used in an extended sense. All remaining echinoids, both regular and irregular, either possess the above characters or are descended from ancestors with them and are included in the subclass Euechinoidea Bronn. In fact, the preceding discussion may be summarized by saying that we propose to transfer the cidarids from the second of these groups to the first.

The passing of the familiar terms "Regularia" and "Irregularia" may be regarded with sorrow by many. But though we have given reasons for terminating their employment in a systematic sense, we shall continue to use them as a form of morphological shorthand.

Attention is drawn to the fact that the ordinal and subordinal names in our scheme are mostly formed from the stem of the name of an included genus with the terminations -oida and -ina respectively. In this we return to the old usage which prevailed before Jackson and Mortensen introduced ordinal names based on morphological features. We have attributed these ordinal names to the first author to use them in latinized form for a category in the class-order group. The nomenclature used is summarized in the appendix.

Subclass PERISCHOECHINOIDEA McCoy, 1849

Diagnosis.—Regular echinoids with interambulacra of 1–14 columns; ambulacra of 2–20 columns, without compound plates; periproct within apical system; perignathic girdle of apophyses only or none; teeth grooved; no branchial slits, no sphaeridia, no ophicephalous pedicellariae.

Remarks.—Originally the order Perischoechinida, including Palaechinidae and Archaeocidaridae and the "lepidocentrid" genus *Perischodomus*. Jackson (1912) altered its scope to include all Paleozoic echinoids except Echinocystoida (here included), *Bothriocidaris* and Archaeocidaridae. We restore the Archaeocidaridae, add the remaining Cidaroida and *Bothriocidaris*, and include all the groups placed in the order Perischoechinoida as used by Jackson.

Order BOTHRIOCIDAROIDA Zittel, 1879

Diagnosis.—Interambulacra of one, ambulacra of two columns; genital plates not recognized; interambulacra not reaching margin of peristome; lantern unknown; madreporite radial.

Family Bothriocidaridae Klem, 1904.

Remarks.—Since its establishment by Jackson in 1896 the systematic position of this order has been the subject of argument, but its content (the genus *Bothriocidaris* alone) has not been modified. The systematic issue has been dealt with above so that further comment is unnecessary.

Order ECHINOCYSTITOIDA Jackson, 1912 (as Echinocystoida)

Diagnosis.—Coronal columns as for subclass; corona imbricate, ambulacral plates imbricating adorally, interambulacral plates adapically and over the ambulacrals along the adradial suture; primordial ambulacral and interambulacral plates in basicoronal row; genital plates certainly present; no perignathic girdle.

Family Echinocystitidae Gregory, 1897, including Lepidocentridae Lovén, 1874, emend. Mortensen, 1935, as a senior subjective synonym.

Remarks.—Jackson's order Echinocystitoida [Echinocystoida] was rejected by Mortensen (II, p. 61) on the ground that its principal differentia—the exocyclic position of the periproct—was based on a misinterpretation (Hawkins & Hampton, 1927, p. 591). We feel that this action is unnecessary and prefer to use Jackson's name. Inasmuch as the periproct of *Echinocystites* is endocyclic, there does not appear to us that there is any criterion by which the families Lepidocentridae Lovén, 1874, and *Echinocystitidae* [Echinocystidae] Gregory, 1897, can be separated. For this family we prefer to use Gregory's name.

Maintenance of the family Lepidesthidae

depends upon whether one adopts Jackson's view (1912, p. 232) that the group is an offshoot from the Palaechinidae, or believes with Mortensen (II, p. 51) that it is inseparable from the Lepidocentridae (=Echinocystitidae). The merging of these two families into one creates a comparatively enormous unit, embracing forms as diverse as *Aulechinus* and *Meekechinus* and lumping together a variety of evolutionary trends. Nevertheless, like Mortensen, we can find no satisfactory basis for subdividing it. It should be remembered that a large majority of the known forms are of Early Carboniferous age, so that the apparent distinctness of some of the older forms may in fact be due to imperfections in the paleontological record. Until more is known of pre-Carboniferous echinoids in general and until the evolutionary radiation of the Lower Carboniferous genera is more fully understood, it would seem best to accept the family Lepidocentridae (=Echinocystitidae) in the wide sense of Mortensen. His family Palaeodiscidae (III, 1, p. 351), established for genera with an open ambulacral furrow (*Aulechinus, Ectinechinus, Palaeodiscus* and possibly *Koninckocidaris* and *Lepidechinoides*) is of questionable value since it is by no means certain that a true ambulacral furrow is present in all these genera.

Mortensen argued persuasively (II, p. 49) for the derivation of post-Paleozoic echinoids from non-cidaroid as well as cidaroid stocks. In particular, he placed the Echinothuriidae with the "Lepidocentridae" in his Lepidocentroida. Previously (Bather, 1909) it had always been supposed that the only connection between Paleozoic and later forms was through the Cidaroida and it cannot be too strongly repeated that no paleontological evidence to the contrary has yet been produced. All known Permian echinoids (except the last known "lepidocentrid," *Meekechinus elegans* Jackson) are cidaroids and all known Triassic echinoids (except Tiarechinidae) are either cidaroids or primitive regulars of manifest cidaroid affinity.

Mortensen's hypothesis, though lacking material support at present, is nonetheless a stimulating one and is certain to influence future studies of Permian and Triassic echinoids. For the present, however, it would seem better to adopt the approach that has proved so successful with the ammonites and, when dealing with specialized groups, to see whether it is not possible with echinoids also "to link up such extremes with some less modified contemporary stock" (Spath, 1933, p. 3). It is not, of course, suggested that echinoid evolution was a copy of ammonoid evolution, either in pace or in pattern; but it is held that, at the family level, it is safer to establish the relationships between the earliest genera and their contemporaries in other families before the wider, and necessarily more speculative connections are regarded as demonstrated.

The particular case of the supposed derivation of Echinothuriidae from Lepidocentridae (=Echinocystitidae) is open to criticism on these lines. Direct comparison is made between the highly specialized Recent forms and their supposed Paleozoic ancestors, ignoring the evidence given by the Jurassic *Pelanechinus*, the earliest echinothuriid. This is almost "a return to that stage in zoological systematics when aquatic mammalia were grouped with fishes on account of similar external shape" (Spath, 1933). When the ontogeny and geological history of the Echinothuriidae are studied, it is clear that their "lepidocentrid" features are the product of adaptive convergence, not of direct genetic transmission. The opinion of Neumayr (1889) and Gregory (1897) that the Echinothuriidae are most nearly related to the Pedinidae is here held to conform most closely with the evidence.

Mortensen stressed the importance to his theory of the following characters:

1. Imbrication of coronal plates. According to Thiéry (1928, op. post.) imbrication persisted in cidarids until at least Bajocian times and it is well known in such Recent genera as *Astropyga*. The form and ornamentation of the plates in *Pelanechinus* are so typically pedinid as to outweigh the importance of their imbricate condition; nor is there any close resemblance in these important characters between the plates of Recent Echinothuriidae and Echinocystitidae.

2. Ambulacral structure. Although some Echinocystitidae may show incipient ambulacral complexity, there is no evidence that this is ever of the diademoid type seen in the Echinothuriidae, which is intimately

linked with the presence of auricles in the perignathic girdle and with the development of large tubercles. The ambulacral complexity of Echinocystitidae is comparable with that of *Paracidaris* or *Rhabdocidaris* but not with that of any of the non-cidarid regular echinoids. In *Pelanechinus* the structure is even an advanced development of the diademoid type. The structures illustrated by Mortensen (II, fig. 53b,c; 54a,b) support this conclusion, as does his own analysis of advanced echinothuriid structure (II, fig. 53a).

3. The structure of the peristome. In adult Echinothuriidae, the peristome is covered by many ambulacral and non-ambulacral plates, as in Echinocystitoida and Cidaroida. Phylogenetic arguments implying direct genetic connection are weakened, however, by Mortensen's own figure (II, fig. 62b) of ten typically "regular" buccal plates in *Kamptosoma* and by his statement (p. 95) that these are present in the young of all echinothuriids. This permits the inference that the condition in adult Echinothuriidae is a secondary development.

4. The absence of branchial slits. These are as strongly developed in *Pelanechinus* as in the contemporary Pedinidae, so that their loss in the Recent genera would seem to be a secondary feature.

5. The tuberculation. In *Pelanechinus*, as well as in some Recent genera, this is of typical pedinid appearance and quite unlike anything seen in Echinocystitidae. Apart from the imbrication, detached plates of *Pelanechinus* would be almost indistinguishable from those of the contemporary *Phymopedina*.

6. The perignathic girdle. Mortensen held that "the existence of auricles of a rather primitive type in the Echinothuriids is by no means proof against [i.e., disproof of] their close relation with the Lepidocentrids" (II, p. 119). The fact remains, however that auricles are unknown in any "lepidocentrid." The internal swellings on the ambulacral plates of *Pholidocidaris* (Bather, 1918) are not homologous, since they are part of the plates on which they sit. In *Pelanechinus* it has been possible to demonstrate the presence of broad, high, widely separated auricles (specimen no. E. 1884 in the British Museum, Natural History) closely similar to those of Phymopedina (Hawkins, 1934, fig. 15, p. 632).

Evidence from *Pelanechinus*, with some from Recent forms, thus shows that it is more likely that the Echinothuriidae originated from some contemporary and closely similar pedinid stock than from the Echinocystitidae, their association with which appears forced and unnatural. The order Echinocystitoida is thus reduced to the single family Echinocystitidae, but its retention is considered justified from the ancestral importance of that family.

Order PALAECHINOIDA Haeckel, 1866 (= Melonechinoida Gregory, 1900, as Melonitoida)

Diagnosis.—Interambulacra of one or more than two, ambulacra of two or more columns; corona rigid, but ambulacra bevel over interambulacra along adradial suture; base of corona resorbed; genital plates present; tubercles imperforate; no perignathic girdle.

Families Palaechinidae McCoy, 1849, Cravenechinidae Hawkins, 1946.

Remarks.—This order, comprising but two families is maintained because of its isolated position and independent line of development.

Order CIDAROIDA Claus, 1880 (as Cidarideae)

Diagnosis.—Interambulacra of two or four and ambulacra of two columns; ambulacra narrow; corona rigid, or imbricating as in Echinocystitoida; base of corona resorbed; genital plates present; one large primary tubercle on each interambulacral plate; perignathic girdle of apophyses only or none; primary radioles with a cortex layer.

Families Archaeocidaridae McCoy, 1849; **Miocidaridae** new name; Cidaridae Gray, 1825.

Remarks.—Mortensen followed established usage by including here two families, Archaeocidaridae and Cidaridae (with subfamily "Streptocidarinae"). It is in this order that he did most to establish the current classification and to destroy the old systematic concepts, and it is here that the greatest divergence has hitherto existed be-

tween the paleontological and zoological viewpoints.

The family Archaeocidaridae McCoy, 1849, is principally known from the Carboniferous and Permian. The interambulacral columns are always more than two in number and the corona is imbricate. These grounds are sufficient, even in ignorance of the structure of the radioles and the nature of the pedicellariae, for continued recognition of the family.

The Cidaridae were divided by Mortensen into "Streptocidarinae" with imbricate and Stereocidarinae with rigid corona. The term Streptocidarinae, however, which dates from Lambert, 1900, is not acceptable as a subfamily or family name, since it is not formed from the name of an included nominal genus. Since it includes principally Triassic genera of which *Miocidaris* is the best known, the term **Miocidaridae** new name, is here proposed in substitution. It is given family rank because of the distinctive character of the imbrication in the more typical genera and on account of its restriction in geological time. It is possible, however, that it is not a phylogenetically homogeneous family. The Liassic species referred to *Miocidaris* by Lambert & Thiéry and the "streptocidarine" genera of Thiéry (1928) may represent more than one lineage running from Archaeocidaridae to Cidaridae.

The family Cidaridae is thus restricted to those Cidaroida that have 20 columns of plates (with the sole exception of *Tetracidaris*) in a rigid corona and is equivalent to Stereocidarinae as used by Mortensen. This latter subfamily was proposed by Lambert (1900, p. 53) with two "tribes" Rhabdocidarinae and Leiocidarinae. The former included the genus *Cidaris* itself. Mortensen (I, p. 68) placed *Cidaris* in the subfamily Stereocidarinae. Thus, nomenclatorially, the Stereocidarinae of Lambert and of Mortensen and the Rhabdocidarinae of Lambert must be replaced by Cidarinae as the nominate subfamily of Cidaridae. Taxonomically, however, both terms may usefully be employed for subfamilies corresponding with the "groups" Stereocidarina and Rhabdocidarina of Mortensen and containing respectively the nominate genera *Stereocidaris* and *Rhabdocidaris*. We propose similarly to treat the remaining "groups" of Mortensen's Stereocidarinae as subfamilies as also the family Psychocidaridae Ikeda, 1935. We accept unreservedly the superiority of Mortensen's classification of cidarids over that of Gignoux (1935), following the convincing application of the former to fossil material by Fell (1954).

Subclass EUECHINOIDEA Bronn, 1860

Diagnosis.—Echinoids with interambulacra and ambulacra of two columns each; corona generally rigid, rarely imbricating; periproct within apical system or not; perignathic girdle of auricles, with or without apophyses, or absent in adult; lantern with grooved or keeled teeth, or absent in adult; branchial slits present, or absent in adult; sphaeridia present; ophicephalous pedicellariae generally present.

Remarks.—Originally included all echinoids except groups equivalent to Echinocystitidae, Palaechinidae and Archaeocidaridae as understood by Mortensen and ourselves.

The wide diversity of trends included in this subclass and the evolutionary relationships to be postulated between the various orders make it desirable to introduce the superorder category. Accepting, with some modifications, the phylogenetic relationships adumbrated, but not applied by Mortensen, we propose to constitute four superorders, as follows: (1) Diadematacea Duncan, 1889, to include the order Aulodonta as used by Mortensen, plus his Echinothuriina and Pygasteridae; (2) Echinacea Claus, 1876, for the orders Stirodonta and Camarodonta as used by Mortensen; (3) Gnathostomata Zittel, 1879, emend., for the Holectypoida (as of Mortensen, but excluding the Pygasteridae), Clypeasteroida, Conoclypina and *Oligopygus* with some other closely related genera of Mortensen's Cassidulidae; (4) Atelostomata Zittel, 1879, emend., for the remaining groups of irregular echinoids (Cassiduloida of Mortensen, with the exceptions noted, and Spatangoida).

Superorder DIADEMATACEA Duncan, 1889

Diagnosis.—Corona rigid or imbricating; tubercles perforate; periproct within apical system or not; perignathic girdle complete in adult: lantern (teeth grooved) present in adult; branchial slits present in adult; com-

pound plates of diademoid structure when present; symmetry of corona approaching radial, never markedly bilateral.

Orders Diadematoida, Echinothurioida, and Pygasteroida.

Remarks.—Following Mortensen, we remove the Hemicidaridae from the group as originally constituted.

Mortensen himself clearly showed his belief that Jackson's orders (originally suborders) Aulodonta, Stirodonta and Camarodonta were not natural groups but grades of evolution which might have been attained independently in diverse stocks. He expressed this belief by retaining the orders but by grouping families held to be of common origin in suborders. Mortensen believed (III, 1, p. 5) that, although both possess aulodont lanterns, his suborders Diademina and Pedinina were of independent origin. We do not accept his derivation of the former from Echinocystitidae but believe in a cidaroid ancestry for both, and propose the elevation of each to ordinal rank. We associate the Aspidodiadematidae with the Diadematidae and Micropygidae in an order Diadematoida.

Order DIADEMATOIDA Duncan, 1889

Diagnosis.—Corona rigid or imbricating; axis of primary radioles hollow; primary tubercles usually crenulate; periproct within apical system; five genital pores; ambulacra with compound plates.

Families Micropygidae Mortensen, 1904; Diadematidae Gray, 1855; Aspidodiadematidae Duncan, 1889.

Order ECHINOTHURIOIDA Claus, 1880 (as Echinothurideae)

Diagnosis.—Axis of primary radioles solid when corona is rigid, hollow when corona is flexible; tubercles smooth; periproct within apical system; genital pores five; ambulacra with compound plates.

Families Pedinidae Pomel, 1883; Echinothuriidae Wyville Thomson, 1872.

Remarks.—In discussing the Echinocystitoida we have explained at length the reasons for associating the Echinothuriidae with the Pedinidae rather than with the Echinocystitidae.

Mortensen also associated the Orthopsidae with the Pedinidae (III, 2, p. 8), basing his conclusion on the perforate, noncrenulate tubercles and the simple ambulacral structure. This involves a belief in the possible derivation of the camarodont lantern from both aulodont and stirodont conditions independently, that is, that the addition of a keel to the teeth and the closure of the foramen magnum had occurred simultaneously in the Orthopsidae, instead of successively as in other Camarodonta. We find it difficult to believe that these two important morphological changes have both occurred twice in the Euechinoidea and prefer to look for an ancestor for the Orthopsidae among the forms included by Mortensen in the order Stirodonta.

Order PYGASTEROIDA, n. order

Diagnosis.—Corona rigid; periproct outside apical system; tubercles smooth; genital pores four; ambulacra without compound plates; axis of primary radioles solid (?).

Family Pygasteridae Lambert, 1900.

Remarks.—In discussing the Early Jurassic irregular echinoids we have explained the reasons for associating the Pygasteridae with the Diadematacea [Aulodonta] and ascribing a pedinoid ancestry to them.

Superorder ECHINACEA Claus, 1876 (as Echinideae).

Diagnosis.—Corona rigid; periproct within apical system; branchial slits present in adult; perignathic girdle complete in adult; lantern present in adult, teeth keeled.

Orders Hemicidaroida, Phymosomatoida, Arbacoida, Temnopleuroida, and Echinoida.

Little is as yet known of early stirodont types and Liassic records of such genera as "*Acrosalenia*," "*Hemicidaris*" or "*Pseudodiadema*" should be treated with reserve unless the presence of keeled teeth is definitely reported. Species of the first two of these genera in the Middle Jurassic have solid radioles and this may possibly indicate near relationship. The early origin of the stirodont condition is indicated by the occurrence in the English lower Lias (lower Pliensbachian) of echinoids with perforate, crenulate tubercles and hollow radioles (the external characters of Diadematidae) and keeled teeth, but this material is not yet sufficiently well known for full description.

Order HEMICIDAROIDA Beurlen, 1937
(as suborder Hemicidarina).

Diagnosis.—Interambulacral plates with a single large tubercle (except in some Orthopsidae) which is sometimes reduced above the ambitus; ambulacra with compound plates of diademoid structure, often only in adoral region; primary radioles with solid axis and a cortex layer (unknown in Orthopsidae); lantern with foramen magnum open except in Orthopsidae; apical system with or without suranal plates.

Families Acrosaleniidae Gregory, 1900; Saleniidae L. Agassiz, 1838; Hemicidaridae T. Wright, 1857; Orthopsidae Duncan, 1889.

Remarks.—The suborder Calycina as used by Mortensen comprises the families Acrosaleniidae and Saleniidae. It may be true that these two are genetically related as has always been supposed but, we think it possible that they may be independently related to the Hemicidaridae. Whichever belief is nearer to the truth, we adopt Beurlen's suggestion of grouping the Hemicidaridae with the Acrosaleniidae and Saleniidae in the order Hemicidaroida Beurlen, 1937 (as Hemicidarina) and add the Orthopsidae as well.

In the search for an ancestor for the Orthopsidae most stirodont families are excluded from consideration because the tubercles are either imperforate, or if perforate are also crenulate, or because of more complex ambulacral structure. In the Hemicidaridae, however, though the tubercles are characteristically perforate and crenulate, they are perforate and non-crenulate in *Tiaridia* and *Cidaropsis*. Further, in *Plesiocidaris*, *Pseudocidaris* and *Gymnocidaris* the ambulacral tubercles, which are perforate and crenulate below the ambitus, are imperforate and smooth above the ambitus. It thus seems that there is a tendency in this family for either the perforate or the crenulate condition, or both, to be lost.

The simple ambulacral structure has been held to preclude the derivation of *Orthopsis* from most of the stirodont echinoids, in which the ambulacral structure is complex. In *O. miliaris* (the type species), although the pore-pairs are uniserial, there is only one tubercle to every three ambulacral plates, indicating at least incipient complexity, while close to the peristome the pore-pairs are arranged in oblique triad arcs. This is even more marked in *O. granularis* (L. Agassiz & Desor) (Text-fig. 1c). In most Hemicidaridae the ambulacral structure is more complex in the adoral than in the adapical region; the condition just described in *Orthopsis* is closely similar to that in *Plesiocidaris* and *Gymnocidaris* (II, fig. 209, p. 401; fig. 201b, p. 385), though less advanced than in the latter. In the latter, the abrupt coarsening of the ambulacral ornament in passing on to the adoral surface typical of most Hemicidaridae is more gradual and is essentially similar to the condition in *Orthopsis*. The apical system is also similar in both families. In both the foramen magnum of the lantern is deep. In *Hemicidaris intermedia* (II, fig. 206b–e, p. 391) the epiphyses nearly meet over the foramen, though not in quite the same manner as in *O. sanfilippoi* (III, 2, fig. 7a, p. 13). Thus, although we cannot point to a particular Hemicidarid ancestor for the Orthopsidae, we consider it at least likely that both are descended from a common ancestor in early Jurassic or even older time.

Order PHYMOSOMATOIDA Mortensen, 1904
(as suborder Phymosomina)

Diagnosis.—No suranal plate; primary radioles usually with solid axis, with or without cortex layer; interambulacral plates generally with more than one smooth tubercle, but one only in some forms and crenulate in Pseudodiadematidae; lantern with foramen magnum open; compound ambulacral plates of diademoid structure, extending above the ambitus.

Families Pseudodiadematidae Pomel, 1883; Phymosomatidae Pomel, 1883; Stomechinidae Pomel ("les Stomechiniens" of Pomel has priority over Mortensen's Stomopneustidae), 1883.

Remarks.—The families of Mortensen's suborder Phymosomina are possibly not a natural assemblage and the Arbaciidae in particular are difficult to associate with any other family. We propose to separate them in an order Arbacioida. His remaining

families (Pseudodiadematidae, Phymosomatidae, and Stomopneustidae) are in all probability naturally related.

Order ARBACIOIDA Gregory, 1900
(as Arbacina)

Diagnosis.—Compound ambulacral plates of arbacioid structure; primary tubercles imperforate, smooth; periproct (?always) covered by four or five large plates; primary radioles with solid axis, cortex layer more or less developed; lantern with foramen magnum open; surface of corona usually covered with an epistroma.

Family Arbaciidae Gray, 1825.

Remarks.—Mortensen suggested (II, p. 526, 544) that the Arbaciidae might be in part derived from the Tiarechinidae and in part from the Hemicidaridae. We prefer to consider them as probable derivatives from the Hemicidarid ancestral stock.

Order TEMNOPLEUROIDA Mortensen, 1942
(as suborder Temnopleurina)

Diagnosis.—Lantern camarodont; compound ambulacral plates of diademoid or echinoid structure; test sculptured or not, if not then branchial slits sharp, more or less deep; primary radioles with solid axis.

Families Glyphocyphidaè Duncan, 1889; Temnopleuridae A. Agassiz, 1872; Toxopneustidae Troschel, 1872.

Remarks.—Mortensen's suborder Temnopleurina appears to constitute a natural lineage and may be raised to ordinal rank as Temnopleuroida. We accept Mortensen's suggestion (III, 2, p. 5) of a probable origin in the Pseudodiadematidae.

Order ECHINOIDA Claus, 1876
(=suborder Echinina Mortensen, 1942)

Diagnosis.—Lantern camarodont; compound ambulacral plates of echinoid structure; corona not sculptured; primary tubercles imperforate, smooth; primary radioles with solid axis, without cortex layer.

Families Echinidae Gray, 1825; Echinometridae Gray, 1825; Strongylocentrotidae Gregory, 1900; Parasaleniidae Mortensen, 1903.

Remarks.—The camarodont families Echinidae, Strongylocentrotidae, Parasaleniidae and Echinometridae are provisionally grouped in an order Echinoida; but we admit ignorance as to the phylogenetic background of these families and do not claim that our arrangement is necessarily a natural one.

There remain of the old subclass Regularia only the families Tiarechinidae and Heterocidaridae. Since no connection between either of these and any other family can at present be indicated with any confidence, we leave them incertae sedis.

Much remains to be done before the relationships of these orders of Echinacea to each other and to the Cidaroida and Diadematacea can be firmly established. It is provisionally suggested that late in the Triassic an aulodont stock evolved from a cidaroid ancestor and gave rise to the Echinothurioida and Diadematoida, and that about this same time this stock gave rise to the stirodont types; that the Hemicidaroida and Phymosomatoida are descended from the same aulodont ancestor; and that the Temnopleuroida and at least some of the Echinoida are derived from the Phymosomatoida.

Superorder GNATHOSTOMATA Zittel, 1879

Diagnosis.—Corona rigid; periproct outside apical system; no compound ambulacral plates; primary tubercles usually perforate and crenulate; radioles hollow; lantern (teeth keeled) and girdle usually present in adult; apical system and peristome usually approximately opposite; branchial slits absent in adult (except Holectypidae and Discodiidae).

Orders Holectypoida and Clypeasteroida.

Zittel (1879, p. 477) divided the irregular echinoids into the Gnathostomata (with a jaw-apparatus) and the Atelostomata (without a jaw-apparatus). In the former group he included the "Echinoconidae," Conoclypidae, and Clypeasteridae. We propose to adopt this term as the name for a superorder. This group we conceive of as including all those irregular echinoids that possess a stirodont lantern in the adult, namely the Clypeasteroida, Holectypoida (restricted) and the Conoclypidae; together with a group of genera including *Bonaireaster* Pijpers, *Haimea* Michelin and *Oligo-*

pygus de Loriol which we group in the family Oligopygidae Duncan, 1889, but which Mortensen placed in the Cassidulidae.

Order HOLECTYPOIDA Duncan, 1889

Diagnosis.—Corona inflated; ambulacra with reduced plates and interambulacral ornament orderly (?except Galeritidae and Conoclypina); ambulacra narrow on oral surface; teeth with lateral flanges.

Suborders Holectypina s.s., Echinoneina, and Conoclypina.

An important character common to the three suborders is the keeled condition of the teeth, but differences in other features appear to us sufficiently important to call for a recasting of the ordinal classification of Mortensen.

In *Holectypus* the auricles are paired, radial structures, entirely analogous to those of the presumed stirodont regular ancestor (Hawkins, 1934, text-fig. 26, p. 642). In *Echinoneus* the auricles are present only in the young stage and are even then recumbent and much reduced, but are still paired and radial (Westergren, 1911, pl. 12). In *Discoidea* (Hawkins, 1917a) the paired auricles are placed outside the ambulacral pores, adjacent to the adradial suture. They are reduced in height and outwardly inclined and are supported from behind by the paired interradial buttresses. Each auricle is connected by suture to an apophysis (the "false ridge" of Hawkins, 1934, who interpreted the structure as an outgrowth from the first paired interambulacral plates of the corona) which is joined by suture to the neighboring auricle of the next pair. The adoral interambulacral region of the corona is thickened behind the apophysis. The condition in *Pyrina* and *Conulus* is similar, but in the latter the auricles are reduced to slender buttresses supporting the apophysis, which is further modified from the condition seen in *Discoidea* for the accommodation of the retractile buccal plates (Hawkins, 1917b). Hawkins considered that a small knob situated on the interradial suture at the margin of the peristome represented the true apophysis of regular forms, but this is an unpaired structure whereas the apophysis in regular forms is a paired structure (Hawkins, 1934, text-fig. 8, p. 624). The girdle in *Galerites* is of similar type but is still further reduced.

Conulus and *Discoidea*, though clearly differentiated (and placed in separate families by Hawkins, 1920, and by Mortensen, IV, 1), have many differences from the Holectypidae in common, not only in the structure of the girdle, but also in their ambulacral structure and interambulacral ornament, as well as in usually smaller periproct and peristome.

The Echinoneidae although lacking a girdle in the adult are closely similar externally to some species of the conulid genus *Pyrina*. We therefore recognize two suborders in Mortensen's order Holectypoida (already restricted by exclusion of the Pygasteridae), namely the Holectypina (family Holectypidae) and the Echinoneina (families Discoidiidae, Conulidae and Echinoneidae). The Galeritidae, though differing from the Holectypoida in their simple adoral ambulacral structure and in the apparent lack of order in their interambulacral ornament, are provisionally associated with the latter suborder.

Suborder HOLECTYPINA Duncan s.s.

Diagnosis.—No petals; auricles radial in position; reduced plates in ambulacra; ornament orderly.

Family Holectypidae Lambert, 1900.

Suborder ECHINONEINA H. L. Clark, 1925

Diagnosis.—No petals; auricles interradial in position or present only in juveniles and then radial; reduced plates in ambulacra (except Galeritidae); ornament orderly (?except Galeritidae).

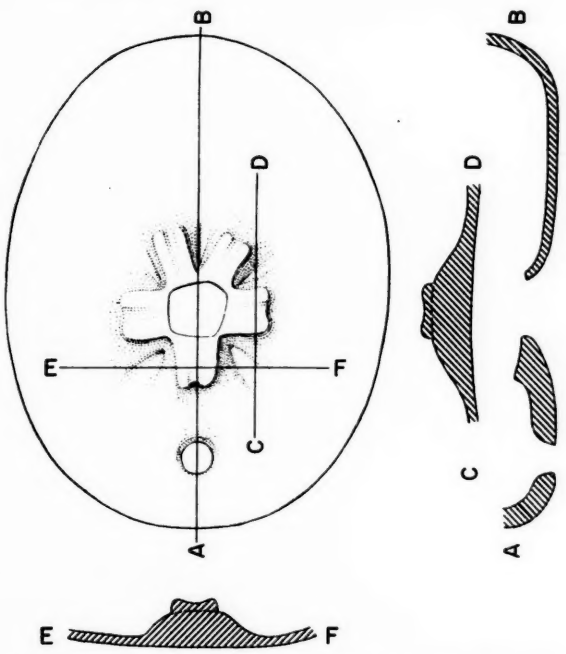
Families Discoidiidae Lambert, 1900; Conulidae Lambert, 1911; Echinoneidae Agassiz & Desor, 1847; Galeritidae Gray, 1825.

Suborder CONOCLYPINA Zittel, 1879

Diagnosis.—Ambulacra petaloid adapically, with reduced plates adorally; auricles interradial; ornament partially at least without apparent order.

Families Conoclypidae Zittel, 1879; Oligopygidae Duncan, 1889.

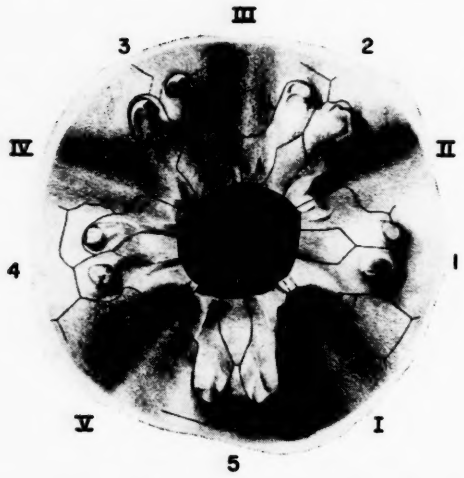
Remarks.—The Eocene genus *Haimea* (Text-fig. 2) differs from the other Holectypoida in having well defined though



TEXT-FIG. 2—*Haimea ovumserpentis* (Guppy). Hypotype, ×1.5; British Mus. (Nat. Hist.), Dept. Geol., no. E 1712a, Diagrammatic sketch of interior showing auricles. A-B, longitudinal section through oral surface and posterior auricle. C-D and E-F, cross-sections through auricles showing relationship to test.

feebly developed petals and in its interambulacral ornament, which seems to be only partly regular in disposition. In shape, however, it closely resembles *Pyrina* (although the peristome is not oblique) and in ambulacral structure it might well be a discoidiid. It has a well-developed lantern in the adult and although the teeth have not been seen, they are keeled in the closely similar contemporary *Bonaireaster*. In both these genera, and in *Oligopygus*, the girdle consists only of structures interradial in position. These consist of flat, rectangular buttresses, interradially elongated, usually bifurcating distally and bevelled off at the peristomial margin. Distally, they grade down into the thickened interambulacral areas, but their limits in this direction are defined by suture and they are also divided longitudinally by suture. In *Bonaireaster* each half of one of these structures can be seen (Text-fig. 3,4) to extend from the ambulacral plates near the adoral end of the ambulacrum. In other words, each structure consists of two pieces, ambulacral in origin and united by suture to the neighboring auricle of the next pair. Each half is considered to be homologous with one auricle of *Discoidea*. The apophysis cannot be definitely recognized. Duncan's family Oligopygidae is used for these genera, which were Cassidulidae to Mortensen. *Pauropygus* Arnold & Clark is considered a subjective synonym of *Haimea* and the genera *Protolampas* Lambert, *Microlampas* Cotteau and *Ovulechinus* Lambert are tentatively associated with *Oligopygus* on the grounds of general external similarity, though their internal structure has not been examined. All these genera differ from Cassidulidae in the absence of a floscelle and of an anal sulcus.

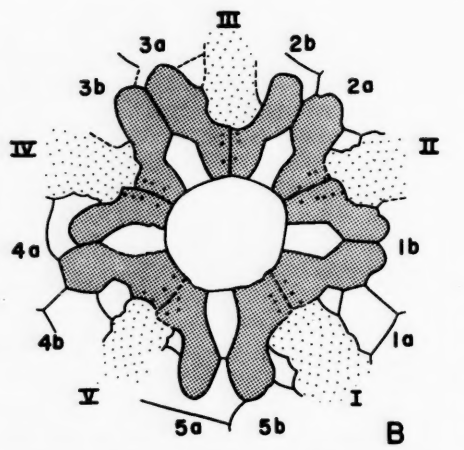
The Conoclypidae have long been known to possess a fully developed lantern in the adult (IV, 1, p. 347), but the girdle seems never to have been seen in an undamaged state until now. In interpreting its structure and homologies, allowance has to be made



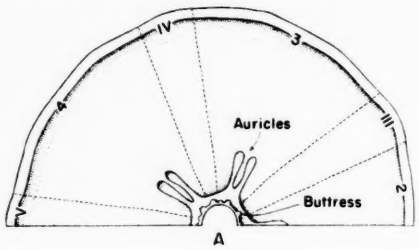
TEXT-FIG. *3*—*Bonaireaster rutteni* Pijpers. Topotype no. 35629, Univ. Calif. Mus. Paleont., ×4.5. View of peristome and auricles from interior, outline of plates indicated.

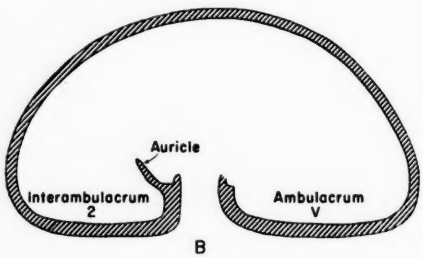
for the extreme development of the infundibulum, or oral funnel in this family, whereby the girdle surrounds a high, vertical wall instead of the shallow, at most slightly invaginated peristome of the Echinoneina and Oligopygidae.

The most striking feature of the girdle (Text-fig. 5) is the elongated, flaring auricles. These are again interradial in position but of ambulacral origin, as in the Oligopygidae. The points of the distal bifurcation, however, are much more prominent and are free nearly to their suturally united bases. The crest of the oral funnel is raised in a thin-walled parapet all around the peristome. It bears a small, battlement-like projection or buttress at each perradial and



TEXT-FIG. *4*—*Bonaireaster rutteni* Pijpers. Same specimen and view as text-fig. 3, showing outline of plates; ×4.5. Auricles densely stippled; ambulacral areas lightly stippled; interambulacral areas not stippled.





TEXT-FIG. *5*—*Conoclypus aequidilatatus* Agassiz. Hypotype, British Mus. (Nat. Hist.), Dept. Geol., no. E 41788-c; ×0.8. *A*, internal view of oral surface, showing auricles and buttresses on peristomial invagination. *B*, vertical section showing peristomial invagination and auricle.

interradial suture. Although the ambulacra are strongly petaloid adapically and although no orderly arrangement of the tubercles has been detected, the adoral ambulacral structure in *Conoclypus* is of the discoidiid pattern and the apical system can readily be imagined as deriving from the discoidiid condition. With these resemblances, especially of the perignathic girdle, in mind, we propose to unite the families Conoclypidae and Oligopygidae in the suborder Conoclypina.

Order CLYPEASTEROIDA A. Agassiz, 1873, emend. Durham, 1955

Diagnosis.—Corona inflated or depressed; apical system monobasal; ambulacra petaloid adapically, wider than interambulacra on adoral surface; secondary tube-feet often extending outside ambulacra; lantern without compass; keeled teeth lacking lateral flanges.

Suborders Clypeasterina s.s., Laganina Mortensen, Rotulina Durham, and Scutellina Haeckel.

The order Clypeasteroida as understood by Mortensen (IV, 2) is here held to be a homogeneous group of holectypoid ancestry (Durham, 1955). It is characterized by a monobasal apical system, ambulacra that are petaloid adapically and wider than the interambulacra on the adoral surface, very numerous secondary tube-feet outside the petals often extending on to the interambulacra, by the lack of a compass in the lantern and by the characteristic keeled teeth that lack the lateral flanges present on all other keeled teeth. The characters of the adapical termination of the interambulacra, the continuity or not of the interambulacra on the oral surface, and the position of the auricles delimit four well marked suborders whose relationships have elsewhere been discussed at length by one of us (Durham, 1955).

Suborder CLYPEASTERINA A. Agassiz s.s.

Diagnosis.—Petals with complex structure and reduced plates; interambulacra discontinuous on adoral surface, terminated adapically by a pair of plates; auricles radial.

Families Clypeasteridae L. Agassiz, 1835; Arachnoididae Duncan, 1889.

Suborder LAGANINA Mortensen, 1948

Diagnosis.—Petals with or without reduced plates; interambulacra continuous on adoral surface, terminated adapically by a single plate or a series of single plates; auricles interradial.

Families Laganidae Desor, 1858; Fibulariidae A. Agassiz, 1873; Neolaganidae Durham, 1954.

Suborder SCUTELLINA Haeckel, 1896, emend. Durham, 1955

Diagnosis.—Corona depressed; no reduced plates in ambulacra; interambulacra continuous or discontinuous on adoral surface, terminated adapically by a pair of plates; auricles interradial; ambulacral food-grooves present.

Families Scutellidae Gray, 1825; Protoscutellidae Durham, 1955; Eoscutellidae Durham, 1955; Dendrasteridae Lambert, 1900; Echinarachniidae Lambert, 1914; Monophorasteridae Lahille, 1896; Mellitidae Stefanini, 1911; Astriclypeidae Stefanini, 1911; Abertellidae Durham, 1955; Scutasteridae Durham, 1955.

Suborder ROTULINA Durham, 1955.

Diagnosis.—Corona depressed, posteriorly slightly to strongly dentate or digitate; no reduced plates in ambulacra; posterior interambulacrum continuous on adoral surface, others variable, all terminating adapically in a series of single plates; auricles interradial.

Family Rotulidae Gray, 1855.

Superorder ATELOSTOMATA Zittel, 1879

Diagnosis.—Corona rigid; periproct outside apical system; lantern, girdle and branchial slits absent in adult; apical system and peristome rarely opposite; no compound ambulacral plates; primary tubercles usually perforate, crenulate; primary radioles hollow; floscelle present or not; interambulacra always wider than ambulacra on ordal surface.

Orders Nucleolitoida Hawkins, Cassiduloida Claus, Holasteroida, n. order, and Spatangoida Claus.

Remarks.—Zittel's (1879, p. 477) Atelostomata, originally proposed for the Cassidulidae, Holasteridae, and Spatangidae we use for a superorder including all remaining groups of the old subclass Irregularia, namely the Cassiduloida and Spatangoida of Mortensen. As already mentioned the oldest known irregular echinoid is *Pygomalus*, a member of Mortensen's Spatangoida. No material is available to us of

the Sinemurian *P. prior* (Desor) and this, coupled with the lack of knowledge of the ontogeny of Jurassic Atelostomata implies an unusually high degree of subjectivity in any phylogenetic speculation. *Apatopygus recens* Milne Edwards has keeled teeth in the young stage (Mortensen, IV, 1, p. 122), but details of the structure of the lantern are unknown in any other member of the superorder, and even the presence of a lantern at any stage in ontogeny is definitely known in only one other instance (*Echinolampas;* Mortensen, IV, 1, p. 287).

Pygomalus and *Galeropygus*, the two oldest Atelostomata, may be independent offshoots from distinct ancestral stocks. Nevertheless, *Galeropygus* appears to be less specialized than *Pygomalus* in its more compact apical system, in the degree of proximity of the periproct to the apical system and in its more radially symmetrical outline. We therefore follow Beurlen (1934, p. 159) in assuming the two genera to have a common ancestor. We regard the former as the oldest known representative of Mortensen's Cassiduloida and the latter as occupying a similar position in the Spatangoida; and the Galeropygidae represent for us the root stock from which all later Atelostomata have diverged.

Order NUCLEOLITOIDA Hawkins, 1920

Diagnosis.—Apical system with disparate genital plates (4 or 5); peristome sometimes opposite apical system; four genital pores; ambulacra usually petaloid adapically, pores of petals usually unequal, petals all similar; floscelle variably developed; no fascioles.

Families Nucleolitidae L. Agassiz and Desor, 1847; Galeropygidae Lambert, 1911, ? Neolampadidae Lambert, 1911.

Remarks.—The assignment of the Neolampadidae to this order is somewhat questionable, but the disparate genital plates of some genera and the lack of phyllodes would seem to relate them more closely to the nucleolitoids than to the cassiduloids.

Order CASSIDULOIDA Claus, 1880

Diagnosis.—Apical system monobasal, with four genital pores; apical system and peristome sometimes opposite; pores of petals nearly equal, petals all similar; floscelle usually well developed; no fascioles.

Families Cassidulidae L. Agassiz & Desor, 1847; Echinolampadidae Gray, 1851.

Remarks.—Attempts to divide the Cassiduloida as used by Mortensen into two orders (e.g., Hawkins, 1929, p. 459) are justifiable in principle and we consider also in practice. Mortensen points out that in the "Echinobrissidae" the apical system includes four genital plates and the pores of the petals are unequal; while in the Cassidulidae and Echinolampadidae there is a monobasal apical system and the pores of the petals are equal. There are admittedly transitions between these conditions, but we nevertheless believe Mortensen's order Cassiduloida to be heterogeneous. The "Echinobrissidae" are certainly related, at least in part, to the Galeropygidae. The Cassidulidae and Echinolampadidae share with the Clypeasteroida a monobasal apical system and a green color when moribund, but we do not consider these features as necessarily indicating a close connection between their respective ancestors.

Mortensen's suborder Conoclypina, together with a revived family Oligopygidae, has already been removed from the Cassiduloida. Of the remainder of this order we place the families Galeropygidae and "Echinobrissidae" in the order Nucleolitoida, characterized by having four or five disparate genital plates and unequal pores in the petals. Mortensen held that the Archiaciidae possibly included specialized descendants from both the "echinobrissid" and cassidulid stocks. This family seems to us to require further study before it can be firmly assigned to any order. We therefore restrict the order Cassiduloida to the families Cassidulidae and Echinolampadidae characterized by a monobasal apical system and equal pores in the petals.

Order HOLASTEROIDA, n. order

Diagnosis.—Apical system elongate or disjunct; plastron feebly differentiated or meridosternous; petals, when present, not impressed, not all similar; no floscelle; apical system and peristome sometimes opposite; fascioles variable.

Families Collyritidae d'Orbigny, 1853;

Disasteridae A. Gras, 1848; Holasteridae Pictet, 1857; Urechinidae Duncan, 1889; Calymnidae Mortensen, 1907; Pourtalesiidae A. Agassiz, 1881; Stenonasteridae Lambert, 1922.

Remarks.—In the order Spatangoida as used by Mortensen we recognize two groups of ordinal rank related independently to the basic stock of the Atelostomata. The first of these, for which we propose to use the name Holasteroida, includes the suborders Protosternata and Meridosternata of Mortensen's usage; the second is his suborder Amphisternata, which we term the Spatangoida.

The suborder Protosternata was proposed by Mortensen (V, 1, p. 6) to embrace the families Disasteridae and Asterostomidae (recte Asterostomatidae). Later (V, 2, p. 563) he reported the amphisternous condition of the plastron in the latter so that the suborder then became coterminous with the family Disasteridae (=Collyritidae of Beurlen, 1934).

Beurlen divided the Collyritidae into three subfamilies of which the Disasterinae were thought to have originated in a Galeropygid stock independently from (and later than) the Pygorhytinae and Collyritinae, which were held to be descended from *Pygomalus*. It may be that he reached this conclusion under the influence of his belief that the Collyritinae gave rise to the meridosternous and the Disasterinae to the amphisternous spatangoids. While we accept the first hypothesis, the second seems difficult of acceptance, since it demands a reversal of evolution in order to produce the compact apical system of the Spatangoida (as here restricted) from the disjunct disasterine condition. As Beurlen noted, the only outstanding difference between the Disasterinae and other Collyritidae lies in the structure of the apical system in which, in the former, oculars II and IV are separated by genital 2 while in the latter these oculars are in contact. It seems simpler to regard the disasterine apical system as derived from the collyritine by posterior enlargement of the madreporite than to imagine the evolution of the spatangoid condition through the closing up of the disasterine. We hold that the ethmophract apical system of such a spatangoid as *Micraster* is not homologous but only homoeomorphous with the apical system of *Disaster*, for in the former the posterior oculars are in contact with genitals 1 and 4 and this is never the case in the latter. Nevertheless, we regard the structure of the apical system of sufficient importance to warrant recognition of a separate family Disasteridae.

Order SPATANGOIDA Claus, 1876

Diagnosis.—Apical system compact, never opposite peristome, genital pores four or less; plastron amphisternous; petals usually impressed, not all similar; fascioles usually present; no floscelle.

Families Asterostomatidae Pictet, 1857; Palaeostomatidae Lovén, 1867; Palaeopneustidae A. Agassiz, 1904; Aëropsidae Lambert, 1896; Toxasteridae Lambert, 1920; Micrasteridae Lambert, 1920; Hemiasteridae H. L. Clark, 1917; Spatangidae Gray, 1825; Lovéniidae Lambert, 1905; Pericosmidae Lambert, 1905; Schizasteridae Lambert, 1905; Brissidae Gray, 1855; Maretiidae Lambert, 1905.

Remarks.—Once Beurlen's (1934) hypothesis of the origin of the amphisternate spatangoids from his Disasterinae is rejected, their origin becomes still more difficult to explain. It seems possible that they may have been derived from some nucleolitoid stock, either from the basic galeropygid radicle (the persistence of which until Cenomanian times is indicated by the genus *Jolyclypus* Lambert) or from some generalized nucleolitid such as *Clitopygus* in which the anal sulcus was feebly developed. The earliest Spatangoida, however, already display the characteristic anteal sulcus and amphisternous plastron. These are the Toxasteridae, and it is a further weakness in Beurlen's hypothesis that the earlier members of this family (e.g., *Toxaster raulini* Agassiz from the Hauterivian of Colombia) are less like *Disaster* than are the later European forms. We are not confident that any suggestions that can now be made as to the origins of this order will stand the test of time and research.

Incertae sedis
Family ARCHIACIIDAE Cotteau & Triger, 1869

Superorder Atelostomata. Assignment to order uncertain, may be an unnatural group containing both cassiduloids and nucleolitoids.

Family HETEROCIDARIDAE Mortensen, 1934

Subclass Euechinoidea, superorder and order uncertain.

Family TIARECHINIDAE Gregory, 1896

Subclass uncertain.

Order MEGALOPODA MacBride & Spencer, 1938

Diagnosis.—Interambulacra without definite columns, plates imbricate; ambulacra in two columns with many pores in each plate; an open radial furrow present; mouth covered by five pairs of oral valves; apical system incomplete.

Family Eothuriidae MacBride and Spencer, 1938.

Assignment to class uncertain.

SUMMARY OF CLASSIFICATION

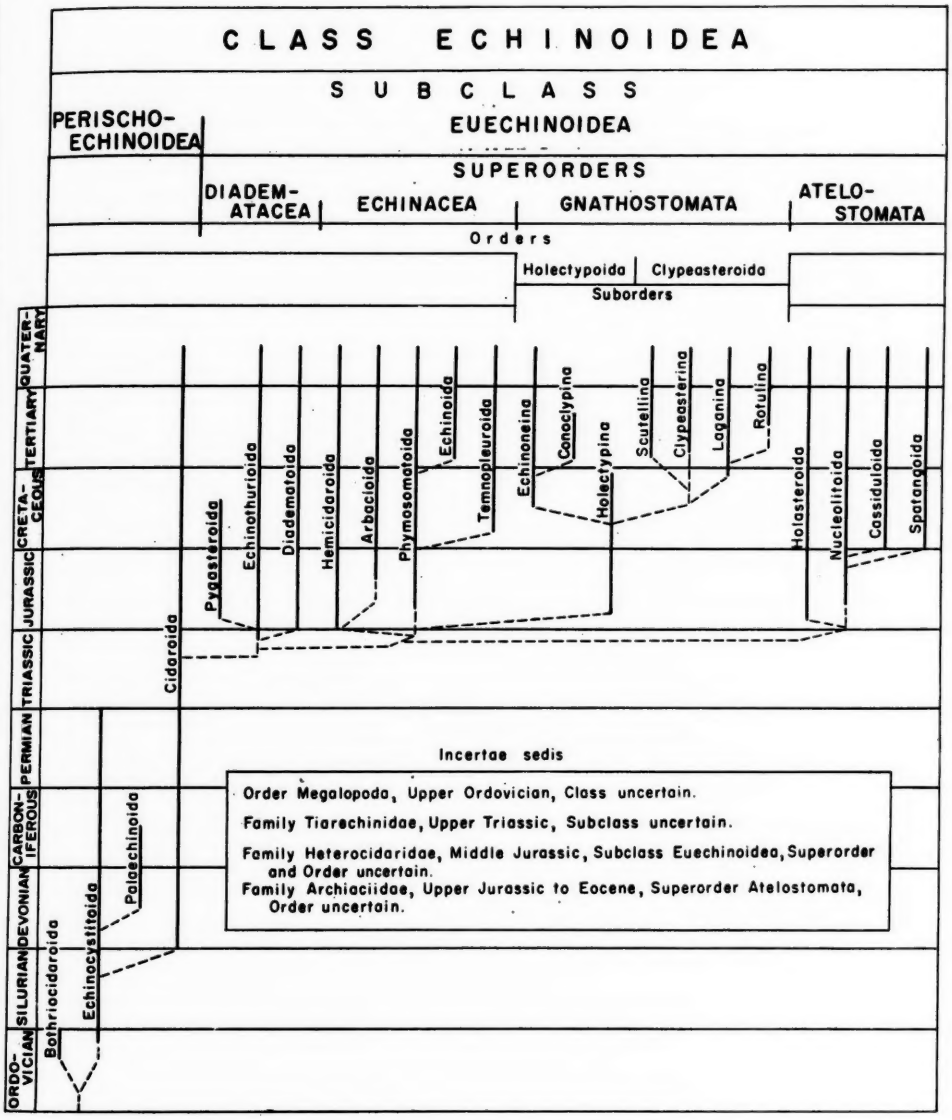
The proposed classification and phylogenetic relationships for the Class as a whole are shown on Text-fig. 6. The relationships and recorded abundances of the families constituting the superorders Diadematacea and Echinacea are presented on Text-fig. 7. The relationships of the families included within the superorder Gnathostomata are indicated in Text-fig. 8. Text-fig. 9 shows the families and postulated or presumed relationships within the superorder Atelostomata.

APPENDIX: ECHINOID ORDER-CLASS GROUP NOMENCLATURE

In considering the names to be used for supra-familial categories in the Echinoidea, we have borne in mind the recommendations published in "Copenhagen Decisions on Zoological Nomenclature" (Hemming, F., ed., 1953), p. 38–43. It is our intention to submit the following material in more extended form to the International Commission on Zoological Nomenclature. We have compiled lists of all the names known to us as having been proposed for these categories, but we have excluded from consideration all those proposed in vernacular words (e.g., Bertrand, 1763; Gras, 1848; Bernard, 1895), all terms consisting of more than one word (e.g., Wright, 1857; Gregory, 1900; Mortensen, II), and names qualified by unaccepted or unplaceable terms such as "Grade," "Series," etc. Names proposed without a named category have been accepted where it is obvious that they fall in the order-class category, and rejected where their rank is uncertain.

The names with which we are concerned all fall within the order-class group defined in the Copenhagen Decisions and we have followed to a limited extent the principle there enunciated regarding family-group names in regarding all names within the group as nomenclatorially co-ordinate with one another; that is to say, we regard a name introduced for a taxon at one level within the group as available with its original authorship and priority at all other levels in the group, but we do not accept the implication that there must be a nominate subdivision of every taxon, since we find that this would lead to undesirable changing of well-established names.

We have had to devise our own solutions for certain problems not covered in the Copenhagen Decisions. One such problem concerns the status of a name, originally proposed in the family-group, which has become attached to a taxon in the order-class group. For example, the familiar names Regularia and Irregularia were originally proposed as subfamily names (Latreille, 1825); Mortensen (IV, 1) uses the same words as subclass names and attributes them to Latreille, 1825. Again, both the family name Clypeasteridae and the order-name Clypeasteroida have been attributed to L. Agassiz, 1835 (whose original usage was in the vernacular). We have concluded that names of this sort should have authorship and priority in the order-class group only from the author and date of their elevation to that group in Latinized form. One reason prompting us to this conclusion is a historical one. Names in the order-class group are generally of later origin than names in the family-group, for the phylum Echinodermata was for long

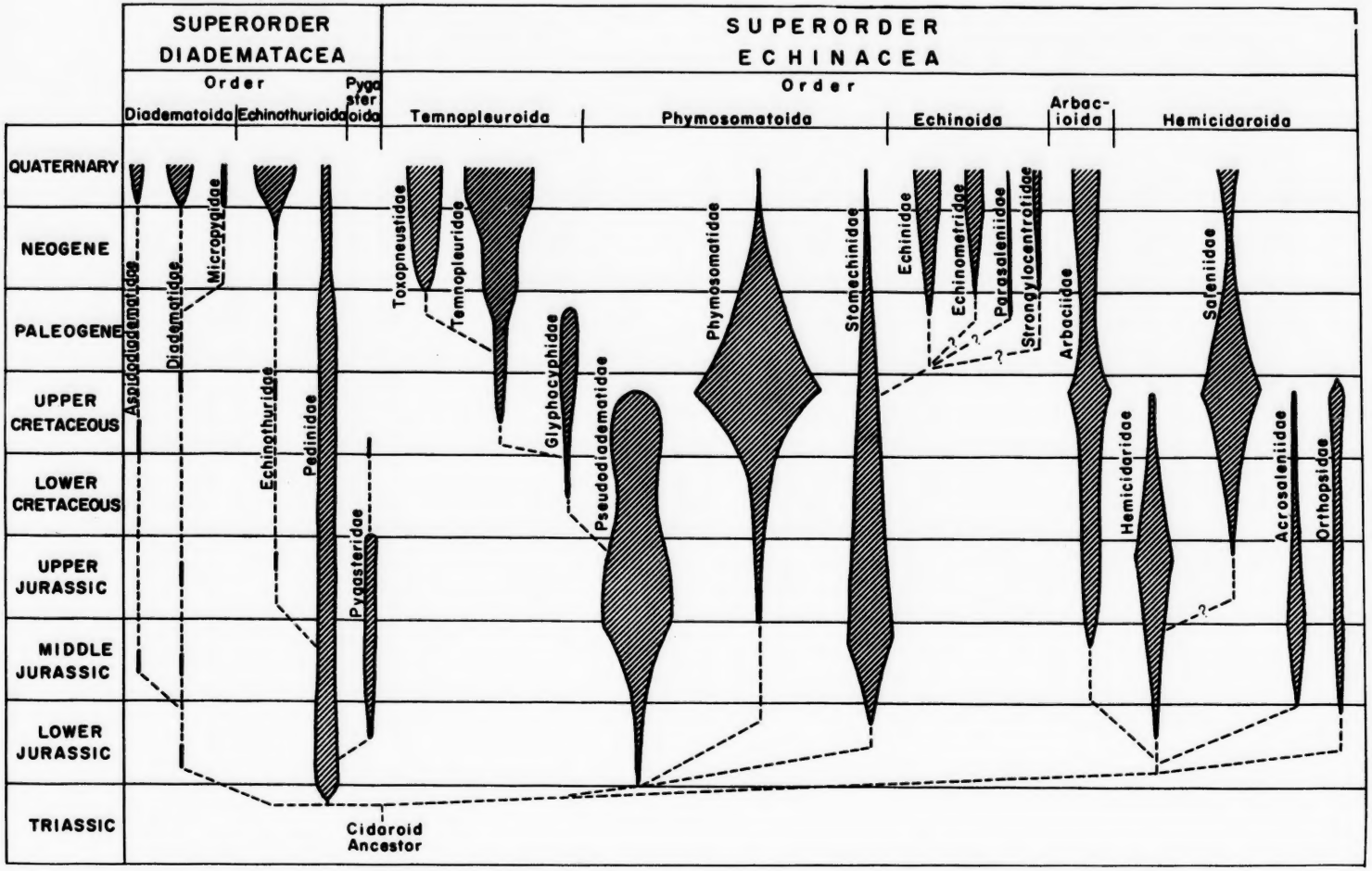


TEXT-FIG. 6—Phylogeny of the class Echinoidea.

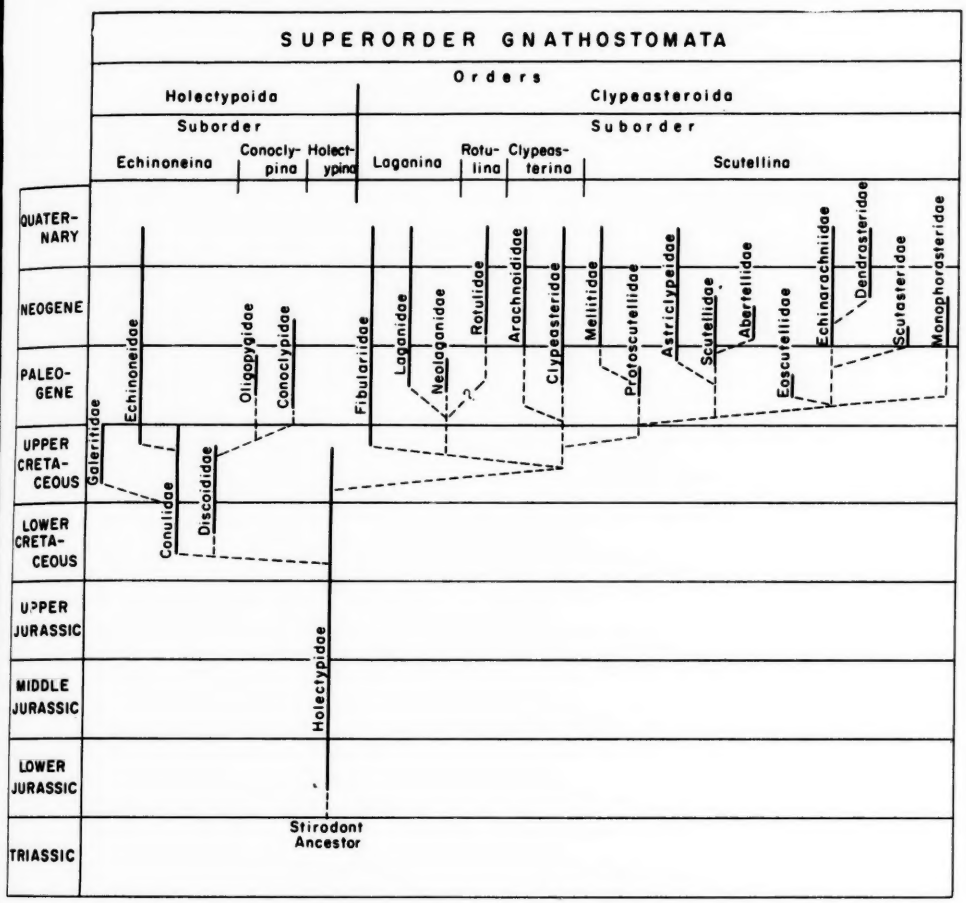
accorded only the status of a class, and the class Echinoidea only that of an order.

With regard to names in the order-class group originally proposed in vernacular form, we have recognized these as available only when they have been published in the Latinized form, and we have attributed them to the author who first so published them.

It is laid down in the Copenhagen Decisions that categories in the order-class group are to be defined by the type concept, the type unit in each case to be a genus. We have assumed as a logical consequence of this, that if a genus is selected as type genus of a taxon at a given level in the order-class group, then that same genus must ipso facto be the type genus of a taxon in every lower category in the group, as



TEXT-FIG. 7—Phylogeny and recorded abundance within the superorders Diadematacea and Echinacea. Width of column indicates relative abundance as based on number of named species.

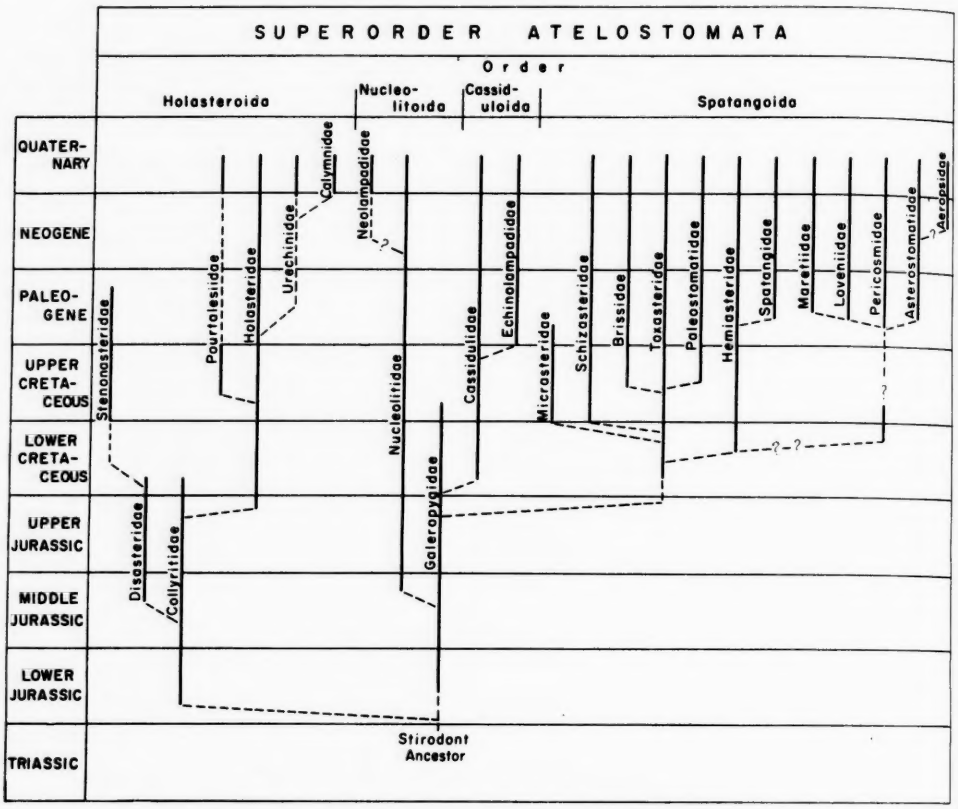


TEXT-FIG. 8—Phylogeny of the superorder Gnathostomata.

well as of taxa in every category in the family-group. The problems raised by this conclusion seem to us less than those which would be raised by any other.

We have had to consider names formed from the stem of the name of the genus which we propose to select as type genus of the taxon concerned; names formed from the stem of the name of an invalid generic homonym; names formed from the stem of the name of a genus which it would clearly be inconvenient or absurd to select as type genus; names formed from the stem of the name of the type-genus, but modified by the addition of a prefix; and names formed from the name of some morphological character thought to indicate close relationship between the forms endowed with it. We consider that names of the first kind are by far the most satisfactory, and we propose to request the International Commission on Zoological Nomenclature to recommend that, in future, the names of newly proposed categories in the order-class group be formed from the stem of the name of the type genus. In particular, we have found that names formed from morphological characters are particularly liable to cause inconvenience, because the taxa they represent are so frequently considered, with advances in taxonomic theory, to include unrelated forms.

Although we have rejected all vernacular names from consideration in the present issue, we have done so with some regret, for certain of these names are familiar to



TEXT-FIG. 9—Phylogeny of the superorder Atelostomata.

all workers in the subject and have long since been given proper Latinized forms. Our decision has involved comparatively little upsetting of familiar names in our own taxonomic scheme, but specialists who disagree with us may find their household words rudely disturbed. It is, of course, open to these specialists to apply to the International Commission on Zoological Nomenclature for the preservation of the names in which they are interested. We take this opportunity, however, of stating that we propose to follow a different course with names in the family-group. In that group, many names of universal and uninterrupted acceptation have always been attributed to the author who first proposed them in a vernacular form and with priority from the date of that proposition. We expressly cite paragraph 53 (2), p. 36 of the Copenhagen Decisions in support of our proposal to adhere to these names as customarily used.

In general we have felt it appropriate to use uniform terminations for ordinal and subordinal names. We have used "-oida" for ordinal and "-ina" for subordinal terminations and corrected all names (except three in each group) we consider available to this format. For superorders we have recognized either "-ata" or "-acea" as appropriate terminations, for subclass either "-ica" or "-oidea," and for the class "-oidea" has likewise been used.

We append a list of all names which we have noted and which we consider to be nomenclatorially suitable in the order-class group in Echinoidea. We have arranged them in alphabetical order under the categories class, subclass, superorder, order, suborder, and we nominate a type genus in every instance. We also list after each

name we consider to be available all other names which we feel should be considered as synonyms (either objective or subjective) and designate type genera for them in accordance with this view.

As a result of our compilation and an appropriate selection of type genera we recommend the following supra-familial nominal categories for use within the class Echinoidea.

Summary of Recommended Order-Class Group Names in the Echinoidea
(Names used in this classification indicated by an asterisk.)

Class name

*Echinoidea Leske, 1778

Subclass names

Endocyclica Bronn, 1860
*Euechinoidea Bronn, 1860
Exocyclica Bronn, 1860
*Perischoechinoidea McCoy, 1849
Pseudoechinoidea Mortensen, 1935

Superorder names

*Atelostomata Zittel, 1879
*Diadematacea Duncan, 1889
*Echinacea Claus, 1876
*Gnathostomata Zittel, 1879

Order names

*Arbacioida Gregory, 1900
*Bothriocidaroida Zittel, 1879
Brachygnata Lambert, 1915
*Cassiduloida Claus, 1880
*Cidaroida Claus, 1880
*Clypeasteroida A. Agassiz, 1873
*Diadematoida Duncan, 1889
*Echinoida Claus, 1876
*Echinocystitoida Jackson, 1912
*Echinothurioida Claus, 1880
*Hemicidaroida Beurlen, 1937
*Holasteroida nov.
*Holectypoida Duncan, 1889
*Megalopoda MacBride and Spencer, 1938
*Nucleolitoida Hawkins, 1920
*Palaechinoida Haeckel, 1866
*Phymosomatoida Mortensen, 1904
*Plesiocidaroida Duncan, 1889
*Pygasteroida nov.
*Spatangoida Claus, 1876
Stereosomata Duncan, 1889
*Temnopleuroida Mortensen, 1942

Suborder names

Amphisternata Mortensen, 1907
Aspidodiademina Mortensen, 1939
Calycina Gregory, 1900
Cassidulina Claus, 1880
*Clypeasterina A. Agassiz, 1873
*Conoclypina Haeckel, 1896
*Diademina Duncan, 1889
Echinina Claus, 1876
*Echinoneina H. L. Clark, 1925
*Holectypina Duncan, 1889
*Laganina Mortensen, 1948
Meridosternata Mortensen, 1907
Orthopsina Mortensen, 1942
Pedinina Mortensen, 1939
Protosternata Mortensen, 1907
*Rotulina Durham, 1955
*Scutellina Haeckel, 1896

The recommended categories, their type genera and nominal categories considered to be synonyms are as follows:

Class name

ECHINOIDEA Leske (1778, as "Ordo Echinus"). Type genus *Echinus* Linnaeus, 1758. Objective junior synonyms are: Adelostella T. & T. Austin (1842), Cirrhi-Spinigrada Forbes (1841), Echinata Fischer [von Waldheim] 1823, Echini Goldfuss (1820), Echinida Fleming (1822), Echinidae Fleming (1828), Echinidea Blainville (1834), Echinides Stark (1828), Echinidia Delage and Hérouard (1903), Echinoida Latreille (1825), Echinoidea d'Orbigny (1852), and all subsequent synonymous usages of these names. *Echinus* Linnaeus, 1758, is here designated as the type genus for each of these nominal categories.

Subclass names

ENDOCYCLICA Bronn (1860). Type genus *Echinus* Linnaeus, 1758. Objective junior synonyms are: Desmosticha Haeckel (1866), Regulares Zittel (1879), Regularia Carus (1863), and all subsequent synonymous usages of these names. *Echinus* Linnaeus, 1758, is here designated as the type genus for each of these nominal categories.

EUECHINOIDEA Bronn (1860): Type genus *Echinus* Linnaeus, 1758. Objective junior synonyms are: Autechinida Haeckel (1866), Echinida W. Keeping (1876), Gnathostomata Lambert (1900; non Zittel, 1879), Neoechinoidea Perrier (1893), Regularia Meissner (1903), Regulariae Delage & Hérouard (1903), Typica Carus (1863), and all subsequent synonymous usages of these names. Echinidae T. & T. Austin (1842) is an objective synonym. *Echinus* Linnaeus, 1758, is here designated as the type genus for each of the preceding nominal categories.

EXOCYCLICA Bronn (1860). Type genus *Spatangus* Gray, 1825. Objective junior

synonyms are: Atelostomata Lambert & Thiéry (1921; non Zittel, 1879), Exocycloida Jackson (1912), Irregulares Zittel (1879), Irregularia Carus (1863), Irregulariae Delage & Hérouard (1903), Petalosticha Haeckel (1866), and all subsequent synonymous usages of these names. Apomesostomi Parkinson (1822) and Pleurocysti Fleming (1828) are objective senior synonyms. *Spatangus* Gray (1825) is here designated as the type genus for all the preceding nominal categories.

PERISCHOECHINOIDEA McCoy (1849, as Perischoechinida). Type genus *Palaechinus* McCoy, 1844. Objective junior synonyms are: Palaeoechinida Perrier (1893), Palaeoechinoidea Parker & Haswell (1897), Palechinida Delage & Hérouard (1903), Palechinoidea Zittel (1879), Perischoechinida W. Keeping (1876), Perischoechinidae Zittel (1879), Perischoechinoidea Bronn (1860), and all subsequent synonymous usages of these names. *Palaechinus* McCoy, 1844, is here designated as the type genus for each of the preceding nominal categories.

PSEUDOECHINOIDEA Mortensen (1935). Type genus *Bothriocidaris* Eichwald, 1859.

Superorder names

ATELOSTOMATA Zittel (1879; non Lambert & Thiéry, 1921). Type genus *Spatangus* Gray, 1825. An objective senior synonym is Pleurocysti Parkinson, 1811, for which *Spatangus* Gray, 1825, is here designated as the type genus.

DIADEMATACEA Duncan (1889, as Diadematoida). Type genus *Diadema* Gray, 1825. Objective junior synonyms are: Aulodonta Jackson (1912), Centrechinoida Jackson (1912), Diademaria Haeckel (1896), Diademida Delage and Hérouard (1903), and all subsequent synonymous usages. Branchiata Ludwig (1882) and Ectobranchiata Ludwig (1886) are objective senior synonyms. *Diadema* Gray, 1825, is here designated as the type genus for all the preceding nominal categories.

ECHINACEA Claus (1876, as Echinideae). Type genus *Echinus* Linnaeus, 1758. Objective junior synonym: Camarodonta Jackson (1912), and all subsequent synonymous usages. Type genus here designated as *Echinus* Linnaeus, 1758.

GNATHOSTOMATA Zittel (1879; non Lambert, 1900). Type genus *Clypeaster* Lamarck, 1801. Catocysti Parkinson (1811; non Fleming, 1828) is a senior subjective synonym. *Echinocyamus* van Phelsum is here designated as the type genus for Catocysti Parkinson.

Order names

ARBACIOIDA Gregory (1900, as Arbacina). Type genus *Arbacia* Gray, 1835.

BOTHRIOCIDAROIDA Zittel (1879, as Bothriocidaridae). Type genus *Bothriocidaris* Eichwald, 1869. Objective junior synonyms are: Bothriocidaroida Duncan (1889), Stenopalmaria Haeckel (1896), and all subsequent synonymous usages. *Bothriocidaris* Eichwald, 1869, is here designated as the type genus for the preceding nominal categories.

BRACHYGNATA Lambert (1915). Type genus *Globator* L. Agassiz, 1840.

CASSIDULOIDA Claus (1880, as Cassidulideae). Type genus *Cassidulus* Lamarck, 1801. Objective junior synonyms are: Asternata Gregory (1900), Cassidularia Haeckel (1896), Cassiduloidea Duncan (1889), Nodostomata Lambert (1915), Procassiduloida Lambert (1918), and all subsequent synonymous usages of these names. *Cassidulus* Lamarck, 1801, is here designated as the type genus for the preceding nominal categories.

CIDAROIDA Claus (1880, as Cidarideae). Type genus *Cidaris* Leske, 1778. Objective junior synonyms are: Abranchiata Ludwig (1882), Cidarida Delage & Hérouard (1903), Cidaridaria Haeckel (1896), Cidaroida Duncan (1889), Cidaronia Haeckel (1896), Endobranchiata Meissner (1903), Entobranchiata Ludwig (1886), and all subsequent synonymous usages of these names. Anocysti Parkinson (1811), and Emmestostomi Parkinson (1822) are objective senior synonyms. *Cidaris* Leske, 1778, is here designated as the type genus for the preceding nominal categories.

CLYPEASTEROIDA A. Agassiz (1873, as Clypeastridae). Type genus *Clypeaster* Lamarck, 1801. Objective junior synonyms are: Anthosticha Haeckel (1896), Clypeasteroida Durham (1955), Clypeastrida Delage & Hérouard (1903), Clypeastridea Claus (1876), Clypeastroida Duncan (1889), Clypeastroidea Ludwig (1886), Exocysta Lambert (1900), and all subsequent synonymous usages of these names. *Clypeaster*

Lamarck, 1801, is here designated as the type genus for the preceding nominal categories.

DIADEMATOIDA Duncan (1889). Type genus *Diadema* Gray, 1825. See superorder Diadematacea for synonymy.

ECHINOIDA Claus (1876). Type genus *Echinus* Linnaeus, 1758. See superorder Echinacea for synonymy.

ECHINOCYSTITOIDA Jackson (1912). Type genus *Echinocystites* Wyville Thomson, 1861. Objective junior synonyms are: Lepidocentroida Mortensen (1934), and all subsequent synonymous usages. Plagiocysta Lambert (1900) is an objective senior synonym. *Echinocystites* Wyville Thomson is here designated as the type genus for these two preceding nominal categories. Other objective senior synonyms are: Cystechinida Haeckel (1896), Cystocidaridae Zittel (1879), Cystocidaroida Duncan (1889), Cystoechinoidea Haeckel (1896), Promelonaria Haeckel (1896), and all subsequent synonymous usages of these names. For these last-named nominal categories *Cystocidaris* Zittel, 1879 (an unnecessary new name for *Echinocystites* Wyville Thomson) is here designated as the type genus.

ECHINOTHURIOIDA Claus (1880, as Echinothurideae). Type genus *Echinothuria* S. Woodward, 1863. Objective junior synonyms are: Echinothurida Delage & Hérouard (1903), Streptosomata Duncan (1889), and all subsequent synonymous usages of these names. *Echinothuria* S. Woodward, 1863, is here designated as the type genus of the preceding nominal categories.

HEMICIDAROIDA Beurlen (1937, as Hemicidarina). Type genus *Hemicidaris* L. Agassiz, 1838.

HOLECTYPOIDA Duncan (1889). Type genus *Holectypus* Desor, 1842. Objective junior synonyms are: Holectypida Delage & Hérouard (1903), Pileatoida Lambert (1900), and all subsequent synonymous usages of these names. *Holectypus* Desor, 1842, is here designated as the type genus for the preceding nominal categories.

MEGALOPODA MacBride & Spencer (1938). Type genus *Eothuria* MacBride & Spencer, 1938. Not certainly an echinoid.

NUCLEOLITOIDA Hawkins (1920). Type genus *Nucleolites* Lamarck, 1801.

PALAECHINOIDA Haeckel (1866, as Palechinida). Type genus *Palaechinus* McCoy, 1844. Objective junior synonyms are: Eocidarida Haeckel (1866), Eurypalmaria Haeckel (1896), and all subsequent synonymous usages of these names. *Palaechinus* McCoy, 1844, is here designated as the type genus of the preceding nominal categories. Melonitida and Eumelonaria Haeckel (1866, based on an invalid generic name) and Melonechinoida Mortensen (1934) are subjective junior synonyms with *Melonechinus* Meek & Worthen, 1860 (*Melonites* Norwood & Owen, 1846; non Lamarck, 1822) as type genus.

PHYMOSOMATOIDA Mortensen (1904, as Phymosomina). Type genus *Phymosoma* Haime, 1853. Objective junior synonyms are: Stirodonta Jackson (1912), and all subsequent synonymous usages. *Phymosoma* Haime, 1853, is here designated as the type genus for the preceding nominal category. Cyphosomina Delage & Hérouard (1903) is a senior invalid objective synonym with *Cyphosoma* L. Agassiz, 1838 (non Mannerheim, 1837) as type genus.

PLESIOCIDAROIDA Duncan (1889). Type genus *Tiarechinus* Neumayr, 1881.

SPATANGOIDA Claus (1876, as Spatangidea). Type genus *Spatangus* Gray, 1825. Objective junior synonyms are: Spatangaria Haeckel (1896), Spatangida Delage & Hérouard (1903), Spatangoida Duncan (1889), Spatangoidea Ludwig (1886), Spatangoidea Duncan (1889), Spatangonia Haeckel (1896), Sternata Gregory (1900), and all subsequent synonymous usages of these names. *Spatangus* Gray, 1825, is here designated as the type genus of the preceding nominal categories.

STEREOSOMATA Duncan (1889). Type genus *Echinus* Linnaeus, 1758. Junior objective synonyms are: Stereodermata Lambert (1900), and all subsequent synonymous usages. *Echinus* Linnaeus, 1758, is here designated as the type genus of Stereodermata.

TEMNOPLEUROIDA Mortensen (1942, as Temnopleurina). Type genus *Temnopleurus* Duncan (1889).

Suborder names

AMPHISTERNATA Mortensen (1907). Type genus *Spatangus* Gray, 1825.

ASPIDODIADEMINA Mortensen (1939).

Type genus *Aspidodiadema* A. Agassiz, 1879.

CALYCINA Gregory (1900). Type genus *Salenia* Gray, 1835. Objective junior synonyms are: Salenina Delage & Hérouard (1903), and all subsequent synonymous usages. *Salenia* Gray, 1835, is here designated as type genus for the preceding nominal category.

CASSIDULINA Claus, (1880). Type genus *Cassidulus* Lamarck, 1801.

CLYPEASTERINA A. Agassiz (1873). Type genus *Clypeaster* Lamarck, 1801. Objective junior synonym: Clypeasterina Durham (1955), with type genus *Clypeaster* Lamarck, 1801.

CONOCLYPINA Haeckel (1896, as Conoclyparia). Type genus *Conoclypus* L. Agassiz, 1839. Objective junior synonyms: Conoclypina Mortensen (1948), and all subsequent synonymous usages. *Conoclypus* L. Agassiz, 1839, is here designated as type genus of the preceding nominal category.

DIADEMINA Duncan (1889). Type genus *Diadema* Gray, 1825.

ECHININA Claus (1876). Type genus *Echinus* Linnaeus, 1758.

ECHINONEINA H. L. Clark (1925). Type genus *Echinoneus* Leske, 1778.

HOLECTYPINA Duncan (1889). Type genus *Holectypus* Desor, 1842.

LAGANINA Mortensen (1948). Type genus *Laganum* Link, 1807.

MERIDOSTERNATA Mortensen (1907). Type genus *Holaster* L. Agassiz, 1838.

ORTHOPSINA Mortensen (1942). Type genus *Orthopsis* Cotteau, 1864.

PEDININA Mortensen (1939). Type genus *Pedina* L. Agassiz, 1838.

PROTOSTERNATA Mortensen (1907). Type genus *Collyrites* Desmoulins, 1835.

ROTULINA Durham (1955). Type genus *Rotula* Schumacher, 1817.

SCUTELLINA Haeckel (1896, as Scutellaria). Type genus *Scutella* Lamarck, 1816. Scutellina Durham (1955) is an objective junior synonym with the same type.

REFERENCES

AGASSIZ, A., 1873, Revision of the Echini, Part III. (Cambridge, Mass.)

ARKELL, W. J., 1951, A classification of the Jurassic Ammonites. Jour. Paleont., vol. 24, p. 354–364.

AUSTIN, T., & AUSTIN, T., 1842, Proposed arrangement of the Echinodermata, particularly as regards the Crinoidea and a subdivision of the Class Adelostella (Echinidae): Ann. Mag. Nat. Hist., vol. 10, p. 106–113.

BATHER, F. A., 1909, Triassic echinoderms of Bakony: Resultate wiss. Erforsch. Balatonsees, Bd. 1, pt. 1, Pal. Anhang, p. 1–288, pl. 1–18.

——, 1918, On *Protoechinus* Austin: Ann. Mag. Nat. Hist., ser. 9, vol. 1, p. 40.

BELL, F. J., 1892, Catalogue of the British echinoderms in the British Museum (Natural History), I: British Mus. (Nat. Hist.)

BERNARD, F., 1895, Elements de Paléontologie, vol. 1, pt. 1, p. 1–512.

BERTRAND, E., 1763, Dictionnaire universel des fossiles propres, et des fossiles accidentels: 2 vols. (La Haye, Pierre Gosse junior et Daniel Pinet.)

BEURLEN, K., 1934, Monographie der Echinoiden-Familie Collyritidae d'Orb: Paleontographica, vol. 30, Abt. A, p. 41–194.

——, 1937, Revision der Seeigel aus dem nordwestdeutschen Jura, II Teil, Die regulären Seeigel: Preuss. geol. Landesanstalt, Abhandl., N. F., Heft 174, p. 1–149, pl. 1.

BLAINVILLE, D., DE, 1822, De l'organisation des animaux: vol. 1, p. i–lix, 1–574. (Paris, F. G. Levrault.)

——, 1834, Manuel d'Actinologie ou de Zoophytologie: 694 p., Atlas of 100 pl. (Paris, F. G. Levrault.)

BOGT, C., 1851, Naturgeschichte der lebenden und untergegangenen Thiere: 719 p. (Frankfurt, J. Rutten.)

BRONN, H. G., 1860, Klassen und Ordnungen des Thier-Reichs, erster Band, Amorphozoen: 434 p., 48 pl. (Leipzig and Heidelberg.)

CARUS, J. V., 1863, *in* Carus, J. V., and C. E. A. Gerstaecker, Handbuch der Zoologie: vol. 2, p. i–vii, 1–642. (Leipzig, Wilhelm Engelmann.)

CLARK, H. L., 1925, A catalog of the Recent sea-urchins in the British Museum: p. 1–278, pl. 1–12.

CLAUS, C., 1876, Grundzüge der Zoologie: 3rd ed., vol. 1. (Marburg and Leipzig.)

——, 1880, Grundzüge der Zoologie: 4th ed., vol. 1. (Marburg and Leipzig.)

CUVIER, G., 1817, Le regne animal distribue d'après son organisation: vol. 4, p. i–viii, 1–255.

DELAGE, Y., & HÉROUARD, E., 1903, Traité de zoologie concrète. Vol. 3, Les Echinodermes: p. i–x, 1–495, pl. 1–53.

DUNCAN, P. M., 1889, A revision of the genera and great groups of the Echinoidea: Linn. Soc. (Zool.), Jour., vol. 23, p. 1–311.

DURHAM, J. W., 1955, Classification of clypeasteroid echinoids: Univ. California Publ. Geol. Sci., vol. 31, p. 73–198, pl. 3–4, 38 fig.

FELL, H. B., 1954, Tertiary and Recent Echinoidea of New Zealand. Cidaridae: New Zealand Geol. Surv., Paleontol. Bull. 23, p. 1–62, pl. 1–15.

FISCHER [von Waldheim], G., 1823, Enchiridion Generum Animalium: p. 1–32. (Moscoviae.)

FLEMING, J., 1822, The philosophy of zoology: vol. 2, 618 p. (Edinburgh, Archibald Constable and Co.)

——, 1828, History of British animals: p. i–xxiii, 1–565. (Edinburgh, Bell, and Bradfutes.)

FORBES, E., 1841, A history of British starfishes and other animals of the Class Echinodermata: 270 p. (London.)

GOLDFUSS, G. A., 1820, Handbuch der Zoologie: vol. 1, p. i–xlvi, 1–696. (Nurnberg, Johann Leonhard Schrag.)

GIGNOUX, M., 1933, Les oursins réguliers fossiles, évolution et classification: Univ. Grenoble, Trav. Lab. géol., vol. 17, fasc. 2, p. 1–125.

GRAS, C. J. A., 1848, Description des oursins fossiles du département de l'Isere, . . . : Bull. Soc. Stat. Isere (Grenoble), vol. 4, 54 p., 4 pl.

GREGORY, J. W., 1897, On the affinities of the Echinothuriidae; and on *Pedinothuria* and *Helikodiadema*, two new genera of Echinoidea: Geol. Soc. London, Quart. Jour., vol. 53, p. 112–122, pl. 7, fig. 1–3.

——, 1900, Echinoidea *in* A Treatise on Zoology, Part III, The Echinoderma," ed. E. Ray Lankester. (London.)

GRIFFITH, E., & PIDGEON, E., 1834, The animal kingdom by the Baron Cuvier, vol. 12, The Mollusca and Radiata, viii, 601 p. (London, Whittaker and Co.)

HAECKEL, E., 1866, Generelle Morphologie der Organismen, zweiter Band: allegemeine Entwickelungs-Geschichte der Organismen: 462 p., 8 pl. (Berlin.)

——, 1896, Systematische Phylogenie, vol. 2, Systematische Phylogenie der Wirbellosen Thiere (Invertebrata): p. i–xviii, 1–720. (Berlin, Georg Reimer.)

HAWKINS, H. L., 1912, Classification, morphology and evolution of the Echinoidea Holectypoida: Zool. Soc. London, Proc., 1912, p. 440–497.

——, 1917a, The perignathic girdle of *Discoides cylindricus* (Lamarck): Geol. Mag., Dec. 6, vol. 4, p. 389–398, pl. 25.

——, 1917b, The buccal armature of *Conulus albogalerus* Leske: Geol. Mag., Dec. 6, vol. 4, p. 433–441.

——, 1920, The morphology and evolution of the ambulacrum in the Echinoidea Holectypoida: Roy. Soc. London, Philos. Trans., ser. B, vol. 209, p. 377–480, pl. 61–69.

——, 1922, *Pseudopygaster*, a new type of the Echinoidea Exocyclica from the Middle Lias of Persia: Geol. Mag., vol. 59, p. 213–222, pl. 9.

——, 1929, In defense of *Bothriocidaris:* Geol. Mag., vol. 66, p. 71–79.

——, 1931, The first echinoid: Biol. Reviews, vol. 6, p. 443–458.

——, 1934, The lantern and girdle of some Recent and fossil Echinoidea: Roy. Soc. London, Philos. Trans., ser. B, vol. 223, p. 617–749, pl. 68–70.

——, 1943, Evolution and habit among the Echinoidea: some facts and theories: Geol. Soc. London, Quart. Jour., vol. 99, p. 52–75.

——, 1946, Cravenechinus, a new type of echinoid from the Carboniferous limestone: Geol. Mag., vol. 83, p. 192–197, pl. 13.

——, & HAMPTON, S. M., 1927, The occurrence, structure and affinities of *Echinocystis* and *Palaeodiscus:* Geol. Soc. London, Quart. Jour., vol. 83, p. 574–603, pl. 44–46.

JACKSON, R. T., 1912, Phylogeny of the Echini, with a revision of Palaeozoic species: Boston Soc. Nat. Hist., Mem., vol. 7, p. 1–443, pl. 1–76.

KEEPING, W., 1876, Notes on the Palaeozoic Echini: Geol. Soc. London, Quart. Jour., vol. 32, p. 35–42, pl. 3.

LAMBERT, J., 1900, Etude sur quelques échinides de l'Infra-Lias et du Lias: Soc. Sci. Hist. Nat. Yonne, Bull., Ann. 1899, vol. 53, pt. 2, p. 1–57, pl. 1.

——, 1915, Description des échinides des terrains Neogenes du Bassin du Rhone. Fasc. IV: Soc. Paleont. Suisse, Mem., vol. 41, p. 155–240, pl. 13–17.

——, 1918, Considerations sur la classification des échinides atelostomes: Soc. Acad. de l'Aube, Mem., vol. 82, p. 25–70.

LAMBERT, J., & THIÉRY, P., 1909–1924, Essai de nomenclature raissonnée des Echinides: 607 p., 15 pl. (Chaumont.)

LATREILLE, D., 1825, Familles naturelles du règne animal: 570 p. (Paris.)

LESKE, N. G., 1778, Jacobi Theodori Klein naturalis dispositio echinodermatum . . . , edita et descriptionibus novisque inventis et svnonomis auctorem aucta: p. 1–278, pl. 1–54. (Lipsiae.)

LOVÉN, S., 1874, Etudes sur les echinoidées: Kongl. Svenska Vetenskaps-Akad. Handlingar, vol. 11, no. 7, p. 1–91, pl. 1–53.

LUDWIG, H., 1882, Ueber Asthenosoma varium Grube und ueber ein neues Organ bei der Cidariden: Zeitschr. für wiss. Zool., vol. 34, p. 70–86, pl. 2,3.

——, 1886, Synopsis der Thierkunde by J. Leunis: 3rd ed., vol. 2, p. i–xv, pp. 1–1231. (Hannover, Hahn.)

MACBRIDE, E. W., & SPENCER, W. K., 1938. Two new Echinoidea, *Aulechinus* and *Ectinechinus*, and an adult plated Holothurian, *Eothuria*, from the Upper Ordovician of Girvan, Scotland: Roy. Soc. London, Philos. Trans., ser. B, vol. 229, p. 91–136.

MCCOY, F., 1849, On some new Palaeozoic Echinodermata: Ann. Mag. Nat. Hist., ser. 2, vol. 3, p. 244–254.

MEISSNER, M., 1903, "Systematik" *in* Ludwig, H., Hamann, O., Meissner, M. and Przibram, H., Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reichs: vol. 2, part 3, book 4, p. 1321–1406.

MORTENSEN, TH., 1904, Echinoidea (1). Danish Exped. to Siam 1899–1900: vol. 2, p. 1–124, pl. 1–7.

——, 1907, Echinoidea. Pt. 2: Danish Ingolf Exped. rept., vol. 4, p. 1–200, pl. 1–19.

——, 1928–52, A monograph of the Echinoidea, vol. I, 1928; vol. II, 1935; vol. III, 1, 1940; vol. III, 2, 1943; vol. III, 3, 1943; vol. IV, 1, 1948; vol. IV, 2, 1948; vol. V, 1, 1950; vol. V, 2, 1951; Index, 1952. (Copenhagen, C. A. Reitzel.)

NEUMAYR, M., 1889, Die Stamme des Thierreiches. Wirbellose Thiere: vol. 1, p. i-vi, 1–603. (Wien und Prague, F. Tempsky.)

ORBIGNY, A. D' 1852, Cours elementaire de Paleontologie et de Geologie stratigraphiques: 3 vols. (Paris, Victor Masson.)

PARKER, T. J., & HASWELL, W. A., 1897, A textbook of zoology: vol. 1, p. i-xxv, 1–779. (London, Macmillan and Company.)

PARKINSON, J., 1811, Organic remains of a former World: vol. 3, p. i–xv, 1–479, pl. 1–22. (London, Sherwood, Neely and Jones.)

——, 1822, An introduction to the study of fossil organic remains: p. i–vii, 1–346, pl. 1–10. (London.)

PERRIER, E., 1893, Traité de Zoologie: fasc. 1–2, p. 1–364. (Paris, Librairie F. Savy.)

PICTET, F. J., 1846, Traité élémentaire de paléontologie: vol. 4, p. i–xiv, 1–476. (Paris, Langlais et Leclerq.)

RAFINESQUE, C. S., 1815, Analyse de la nature ou tableau de l'univers et des corps organises: 224 p. (Paris.)

SCHMIDT, F., 1874, Miscellanea Silurica II. Ueber einige neue und wenig bekannte baltisch-Silurisch Petrefacten: Acad. Imp. Sci. St. Pétersbourg, Mem., ser. 7, vol. 21, no. 11, p. 1–48, pl. 1–4.

SPATH, L. F., 1935, The evolution of the Cephalopoda: Biol. Reviews, vol. 18, p. 158–181.

SPENCER, W. R., 1951, Early Paleozoic starfish: Roy. Soc. London, Philos. Trans., ser. B, vol. 235, p. 87–129, pl. 2–8.

STARK, J., 1828, Elements of natural history: vol. 2, p. 1–515, pl. 5–8. (Edinburgh, Adam Black and John Stark.)

THIÉRY, P., 1928, (op. post., ed. Lambert and Cuenot). Considerations phylogenetiques sur les Cidaridae: Archives de zool. expérim. et gen., Notes et Revue, no. 4, p. 179–181.

WAD, G., 1803, Begyndelsesgrunde i Dyrhistorien af Georg Cuvier: vol. 2, 512 p., 7 pl. (Kiobenhavn, N. Moller og Son). Index in Danish, French and Latin.

WESTERGREN, A. M., 1911, Echinonëus and Micropetalon: Mus. Comp. Zöol. Harvard Coll., Mem., vol. 39, p. 34–66, pl. 1–31.

WRIGHT, T., 1851, An introduction to geology and its associate sciences, mineralogy, fossil botany and conchology and paleontology by the late S. F. Richardson, F.G.S., A new edition, revised and considerably enlarged: p. i–xvi, 1–508. (London, H. G. Bohn.)

ZITTEL, K. A., 1879, Handbuch der Paleontologie, I Band, Paleozoologie: Abt. 1, p. 308–560 (Echinodermata). (Leipzig.)

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AGE-CURVE ANALYSIS OF ANGIOSPERM FLORAS

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ABSTRACT—Using data from only 32 Cretaceous and Tertiary floras in the United States, Barghoorn constructed three graphs to show the percentage of genera in each flora which are (1) still "native" to the region of the fossil locality, (2) now "exotic" to the area, or comprise (3) unidentified, extinct, or form-genera. He and others believe that by determining the percentages of these categories in a flora of unknown age, and relating them to the age-curves he has drawn, that its age can readily be determined.

There are so many weaknesses in the method that the graphs can not be used for age assignment. Criticisms of the statistical data involve (a) unreliable basic data, (b) non-significance of the curves, (c) dual age possibilities, and (d) the sample. Paleobotanical weaknesses of the method are outlined in terms of (a) the categories chosen, (b) the factor of geographic position, and its effect on environmental change, (c) migration, (d) latitudinal relations, (e) altitudinal relations, and (f) relict environments.

INTRODUCTION

Several years ago there appeared in this journal a paper reviewing the age and environment of North American angiosperm floras (Barghoorn, 1951). In it Barghoorn analyzed 7 Upper Cretaceous and 25 Tertiary floras in terms of their generic composition. The genera for each flora were grouped into three categories: (1) "native," or those now living in the region of the fossil locality, (2) "exotic," or those not now represented in the area of the fossil site, and (3) those which are either unidentified, extinct, or designated as form-genera. The percentage of the three categories in each of the 32 floras was determined, and these quantitative data were related to age. The data were assembled in the form of three graphs or "age-curves."

The graphs show there is a broad correlation between increasing age and the percentage of "native" to "exotic" genera. The "native" genera show a gradual decrease between the Late Cretaceous and the Late Eocene; this corresponds to the period of northward migration of the Neotropical-Tertiary Geoflora in response to warmer climate, and the displacement of "native" genera to somewhat higher, cooler latitudes. The "native" genera rapidly increase between the Early Oligocene and the Late Pliocene; this reflects the cooling climate of post-Early Tertiary time, and the southward shift of the temperate Arcto-Tertiary Geoflora which displaced subtropical forests at middle latitudes. The "exotic" group finds its maximum in the Late Oligocene; this apparently expresses the ecotonal relationships of the temperate and tropical geofloras across central North America at that time. The "exotic" group rapidly decreases during the later Cenozoic as present day climates came into existence. The shifting percentages of these categories thus express in a broad way the well-known migrations of the Tertiary Geofloras in response to changing climate during the Cretaceous and Tertiary (Chaney, 1947).

However, Barghoorn believes that the age of a flora can be determined by ascertaining the percentages of "native" and "exotic" genera in it, and plotting the data on the age-curves he has constructed. These graphs have been discussed in another paper by Barghoorn (1953), and they seem to have received tacit acceptance by some paleobotanists in this country as a suitable means of age analysis. At least in referring to the method, neither Dorf (1954) nor Scott (1954) have criticized it. Furthermore, Traverse (1955) has used the graphs to show that the Brandon flora is of Late Oligocene to Early Miocene age. Since other investigators may be considering the method seriously in terms of age analysis, it seems desirable to subject it to a brief, but critical scrutiny. Actually, there appear to be a number of statistical as well as botanical reasons why these age-curves are misleading in terms of age determination.

STATISTICAL

Unreliable basic data.—The basic data on which the graphs have been assembled are unreliable for more than half of the 32 floras used in the analysis. Barghoorn chose the genus rather than the species as the basic unit for evaluation because he believes this category "is far less susceptible to mistaken botanical identification and to misinterpretation than is the species" (1951, p. 741). This may be true in some instances, but scarcely meets the facts for many of the floras he analyzed.

The figures Barghoorn presents for the Mascall flora show they fall near the curve he has drawn. However, a revision of this flora (Chaney & Axelrod, in press) indicates his percentages are far off. The figure for "exotic" genera should read 63 instead of 38 per cent, a figure which falls well above the graph he has drawn (fig. 2[1]). The flora has only 37, not 58 per cent "native" genera, which would give it either an early Late Cretaceous, or an Early Miocene age on the basis of the age-curve (see below, Dual age possibilities). He used the data presented by Berry for the Latah flora, yet revisions of the flora (Brown, 1937; 1940; 1946; Chaney & Axelrod, in press) show the "exotic" genera comprise 72 instead of 40 per cent, and the "native" genera represent 28 rather than 34 per cent of the assemblage. Applying the new data to the curves (fig. 1,2), the figures for the "exotic" group again falls far above the high point on the graph. The figure of 28 per cent "native" genera also fits two points on the age-curve, mid Late Cretaceous and Late Oligocene (see below, Dual age possibilities). Several other Middle to Late Tertiary floras he has charted show the same relationships, for their generic lists are not correct botanically.

In the case of the Late Cretaceous to Early Tertiary subtropical to warm temperate Woodbine, Tuscaloosa, Vermejo, Laramie, Raton, Wilcox, Clairborne, and Alum Bluff floras, which have not been revised since they were first described, a large number of the generic determinations are in error; the lists of synonyms which Roland W. Brown (manuscript) has assembled for some of these floras is indeed impressive, not only for species but for genera as well. The poor taxonomic status of these floras at the present time is clearly reflected in the curve (fig. 3) which shows that 15 of the 32 floras selected for study have from 30 to over 60 per cent of their genera in the category of unidentified, extinct or form-genera. Some of these genera may well be extinct, but others are not; form-genera are often identifiable on the basis of extended herbarium studies, and many of those in the unidentified group can be determined in the same way. Identification of the genera in the unknown, extinct or form-genera category (fig. 3) places them in either the "native" or "exotic" class, and hence increases their percentages. One indeed wonders how we might otherwise explain that the Goshen and Comstock floras have less than 10 per cent, whereas the Jackson and Green River floras of generally similar age have from 35 to 55 per cent of their genera in this catetory. Until these Late Cretaceous and Early Tertiary floras, which make up nearly half of the sample analyzed by Barghoorn, have been thoroughly revised, any statistical data based on them are greatly misleading. In brief, an age curve method such as is proposed by Barghoorn can be applied only to floras whose generic lists are sound taxonomically.

Non-significance of curves.—Let us assume for the moment that the percentages of the different categories calculated by Barghoorn are essentially correct. The percentages of "exotic" genera (fig. 2) and "unidentified and extinct genera" (fig. 3) as plotted are so scattered that the age-curves he has drawn scarcely seem to have any statistical significance.

It is also apparent that the curves have such flat crests that they do not have any real stratigraphic value for long spans of geologic time. The graph (fig. 1) of percentage of genera "native" to the region of the fossil locality shows only a five per cent change during the interval from the Late Cretaceous to the Middle Oligocene. The graph (fig. 2) for the "exotic" group shows a five per cent change from the Early Eocene to the Middle Miocene. And the age-curve for the unidentified, extinct or form-genera class (fig. 3) displays a five per cent change from the early Late Cretaceous to the Mid-

[1] Figure references are to Barghoorn, 1953.

dle Eocene. If paleobotanists regularly identified all their species correctly as to genus, then close age determination on the basis of these flat crests might be possible. However, if we have made only a five to ten per cent error—and this is better-than-average—in the generic determinations of a fossil flora which we have just described as new, then on each of the age-curves we are immediately involved with a time-span error of 50 million years, representing the interval from the early Late Cretaceous into the Oligocene. This can scarcely be considered acceptable precision in dating a fossil flora.

Dual age possibilities.—Examination of the graphs shows that the same percentage of genera representing the "native" and "exotic" groups often appear on the Cretaceous, as well as the Tertiary side of the age-curve. For example, Barghoorn's figure 1 shows 35 per cent "native" genera are to be expected in the early Late Cretaceous as well as in the Miocene. The "exotic" group comprises 25 per cent in the early Late Cretaceous, and in the Pliocene as well. From these figures alone we can not decide whether a flora of unknown age is early Late Cretaceous or Middle to Late Tertiary.

Traverse (1955) fell into this trap in dating the Brandon flora. On the basis of his identification of 28 per cent "native" genera in the flora, he concluded the Brandon is Late Oligocene or Early Miocene (Traverse, 1955, fig. 5). But the "well-controlled curve" referred to by Traverse does not date the Brandon as Late Oligocene or Early Miocene, for 28 per cent "native" genera are represented also on the Upper Cretaceous side of the age-curve. Furthermore, the 37 per cent "exotic" genera in the flora matches the Upper Miocene as well as the Cretaceous-Tertiary transition. Traverse presumably discriminated between these possible age assignments (Late Oligocene, mid-Late Cretaceous, Cretaceous-Tertiary transition, Late Miocene) on the basis of 33 per cent extinct or unidentified genera (fig. 3). But this argument carries no weight, for the curve has doubtful validity both statistically as well as botanically, as noted above. Furthermore, as members of this group are identified they will fall either into the "native" or "exotic" categories. This may appreciably alter the percentages of both groups, and hence any age assignment. Again the question may be raised as to why the "Late Oligocene" Brandon flora on the east side of the continent has 33 per cent in this group, whereas the Late Oligocene Bridge Creek flora on the west side has only 10 per cent. It is apparent that the age of the Brandon flora has not been satisfactorily dated by means of these age-curves which purport to show for a continental region the shifting percentages of "exotic," "native," and "unidentified or extinct" genera in Cretaceous and Tertiary floras.

Sample.—1. One wonders why Barghoorn considered only 32 floras, 5 of Cretaceous and 27 of Tertiary age. Many others are available for analysis, including the following:

Cretaceous: Raritan, Magothy, Matawan, Black Creek, Black Buttes, Fox Hills, Dakota, Fruitland, Judith River, Cheyenne, Dawson, Trinidad, Frontier, Mesaverde, Hell Creek, Colgate, Ericson-Almond.

Lower Tertiary: Wasatch, Brandon, Clarno, Swauk, Puget, Evanston, Livingston, Hannah, Fort Union, Barilla Mts., Animas, Chalk Bluffs, Florissant.

Middle Tertiary: Missoula, Grays Ranch, Elko, Republic, Grand Coulee, Whitebird, Eagle Creek, Payette, Salmon, Upper Cedarville, Trout Creek, Blue Mountains, Succor Creek.

Late Tertiary: Beaver Co., Ellensburg, Troutdale, Dalles, Table Mountain, Anaverde, Piru Gorge, Napa, Creede, Alvord Creek, Thorn Creek.

It is apparent that by neglecting these 54 floras, Barghoorn's curves are not based on an adequate sample. If the percentages of the genera in the three categories were assembled and plotted for these floras, which would more than double the size of the sample, is it not possible they might display such a scattering of points that the age-curves would show even less statistical significance than they now appear to have?

2. The floras are not always comparable in terms of an adequate sample of past vegetation, or of time. Some of them, such as those of the Wilcox or Claiborne groups, comprise numerous species from many localities and in several formations. Others are based on small collections from a few inches of strata.

3. The percentages of the three categories may be quite misleading in the case of the smaller floras which have not been sampled adequately. Further collecting at these sites should yield additional plants, which would tend to alter the proportions of genera in each category, and hence the shape of the age-curves.

BOTANICAL

Under this heading are included several criticisms of the method which involve principles governing the interpretation of fossil plants in terms of the categories selected for study, and in respect to various paleoecological and distributional problems.

Validity of categories.—1. Genera vs. species. Barghoorn made the genus the basic unit for age analysis primarily because he believes it is much less subject to misidentification than the species (1951, p. 741). As mentioned above, this supposition is not supported by the evidence in the case of the floras described several decades ago which he has analyzed and whose generic lists are not botanically sound. But even if it were true, such a procedure completely neglects the critical fact that a number of wide-ranging genera are represented by species that *differ greatly* in terms of their environmental relations, and hence in their age significance. For example, species of maple (*Acer*), alder (*Alnus*) birch (*Betula*), hackberry (*Celtis*), hawthorne (*Crataegus*), cottonwood (*Populus*), cherry (*Prunus*) and willow (*Salix*), still live in eastern Oregon near some of the fossil localities in which these genera are recorded in Miocene rocks. They appear on his graph as "native" genera. However, the nearest living relatives of these fossil species do not occur in Oregon or elsewhere in the far West, but in eastern North America and in northeastern Asia, in regions of ample summer rainfall. Thus they should be considered as part of the "exotic" group, having just as much environmental (summer rain climate), and hence age, significance as the "exotic" genera *Carpinus, Cercidiphyllum, Fagus, Ginkgo, Nyssa, Taxodium, Ulmus* and *Zelkova* which lived with them in these Miocene floras. It is no coincidence that the modern descendants of these "exotic" species and genera often live side by side in the summer-wet eastern parts of the northern continents.

2. Native vs. exotic genera. Barghoorn attaches greater stratigraphic significance to the age-curve of "native" genera (fig. 1) principally because, he says, "it is this 'native' element of the fossil flora in which the error of identification is at a minimum" (1951, p. 740). One need only glance at the lists of revisions made of Cretaceous and Tertiary floras in recent years to see that many of the genera initially identified in these floras as "native," are actually "exotic" types (for example, see MacGinitie, 1953; Dorf, 1942; Chaney & Axelrod, in press; Brown, 1937, 1939). Since over half of the floras he has analyzed are in need of a thorough botanical (generic) revision, the presumed stratigraphic value of this "well controlled curve" (Traverse, 1955, p. 22) is highly suspect.

From the standpoint of age analysis, both units must be analyzed carefully. In general, the percentage of "exotic" types (both species and genera) gives us a better estimate of past environment because they reflect a different climate than that of the "native" group near the locality today. Thus the "exotic" group effectively measures the difference between the past and present climate, and hence the age differential it implies. Nonetheless, the percentage representation of the "exotic" group often depends as much on geographic position as on age, for these types have regularly persisted as relicts, either near the ocean or in the mountains, long after they have disappeared elsewhere on the nearby continent (see below, Relict environments).

Geographic position.—The floras analyzed by Barghoorn come from localities scattered widely across the United States, from the Pacific to the Atlantic shore, and from near the Canadian border almost to the Gulf of Mexico. By grouping all these floras together into graphs showing shifting percentages of "native" and "exotic" genera during the Cretaceous and Tertiary, Barghoorn must of necessity believe that the rate of environmental change has been the same throughout this broad region, and that its effect on the percentage of genera in each category has been equal everywhere. This is far from the truth. In general, floras in coastal areas have undergone much less rapid change than those of the interior. Furthermore, the east and west coasts show important differences

in terms of climatic trends, and hence in the evolution of floras. Two examples of the importance of geographic position in terms of its effect on floristic evolution are discussed below, for they make it clear that fossil floras can not be combined into a single graph showing shifting percentages of "native" and "exotic" genera for a continental region, or even for a major part of one.

1. Coast vs. interior. Whereas the central California coastal area was occupied by warm temperate to temperate forests during much of the Middle and Late Cenozoic, in central Nevada there was a progression from temperate forest, to woodland, to steppe, and finally to desert vegetation in the same interval. Floras from the interior region of more rapid environmental change thus have a larger number of "exotic" types. Hence they appear to be older than floras in those geographic regions where conditions have been relatively more stable in terms of rate of environmental change. For example, if we use Barghoorn's data to determine the age of four Mio-Pliocene (early Clarendonian) floras in western Nevada, we find that out of 65 woody plants 16 per cent of the genera are "native," and 84 per cent are "exotic" (Axelrod, 1956). Turning to the graphs drawn by Barghoorn, the age-curve for the "native" genera makes the floras Middle Eocene. The "exotic" group falls far above the age-curve, near the Comstock and Goshen floras of Late Eocene age (see Barghoorn's fig. 2). By contrast, the Mio-Pliocene (early Clarendonian) San Pablo flora from coastal California, which is contemporaneous with these Nevada floras, has 40 per cent "native" and 60 per cent "exotic" genera, which makes it Upper Miocene on the age-curves. The differences in these quantitative relationships reflect the relative degree of environmental change in these regions since the floras were living, and not a difference in age.

2. East vs. west sides of continents. It is instructive to compare the Late Oligocene Bridge Creek flora of eastern Oregon with the Brandon flora of Vermont which has been considered of the same age on the basis of its age-curve relationships (Traverse, 1955). The Brandon flora shows relationship to vegetation now in the Gulf States, but the Bridge Creek has greater affinity with the warm temperate forests of eastern Asia. The comparative percentages of the groups in the floras are as follows:

Native: Bridge Creek—19%, Brandon—29%
Exotic: Bridge Creek—75%, Brandon—37%
Unidentified or Extinct: Bridge Creek—6% (2 genera), Brandon—34%

It is apparent that on the basis of the age-curves these floras can not very well be of the same age. Some of the discrepancy is due to the fact that the basic data for the age-curves are not reliable, as noted above. As compared with the figures presented, the unrevised Bridge Creek data given by Barghoorn are as follows:

Native: 56%
Exotic: 41%
Unidentified or extinct: 4%

But some of the difference is due to the fact that there has been greater climatic, and hence floristic, change on the west as compared with the east side of the continent. The Bridge Creek area now has a summer-dry climate instead of one characterized by rain throughout the year, and winters are appreciably colder. The climate of the Brandon area today differs from that of "Oligocene" time chiefly in having cooler seasons.

Finally, it may be noted that by using the age-curve method, the Mio-Pliocene floras of western Nevada mentioned above (84% "extinct," 16% "native") would be slightly older than the Late Oligocene Bridge Creek flora (75% "exotic," 19% "native"). We reiterate, this reflects not a difference in age, but geographic position and its influence on changing climate, and hence on the relative degree of floristic change in the respective areas since the floras were living. It is apparent, therefore, that the age-curves are greatly misleading. Not only has the factor of geographic position and its control on rate of floristic change been ignored, but floras from coastal and interior regions, and from east and west coasts, have been combined into single graphs for the "exotic" and "native" categories.

Latitude.—The method provides no way to compensate for the important effect of latitude. The Wilcox flora (considered as a group) was laid down near the shores of a

sea that stretched from southern Illinois southward through east-central Texas and into Mexico, across 15° of latitude. The Wilcox flora in the Illinois-Tennessee area includes a large exotic element of warm temperate to subtropical genera. If we could get a sample of the Wilcox flora from northeastern Mexico, however, we probably would find that many of the genera are represented in the subtropical forests that survive in the nearby mountains today. This would tend to give us two age assignments for the Wilcox flora. The sample in the north with a higher percentage of "exotics" would be older than the one in the south, where the same genera would now be members of the "native" category.

Migration factor.—It is well established that the Tertiary Geofloras showed changes in composition and in geographic position during the period. These changes, which were due in large part to changing climate, provide us with a sound basis for estimating the age of a fossil flora representing any one of the major geofloras. However, if we follow Barghoorn's method of analysis it would not be possible to discriminate between various parts of a migrating and evolving geoflora. For example, the Arcto-Tertiary Geoflora was richly represented in Oregon and in central California during the Middle and Late Tertiary. Among its typical floras are the Mascall of eastern Oregon (Chaney & Axelrod, in press) and the San Pablo of west-central California (Condit, 1938). The floras are closely similar, both representing swamp-cypress forests. The comparative figures for the categories proposed by Barghoorn are as follows:

Native: Mascall—37%, San Pablo—40%
Exotic: Mascall—63%, San Pablo—60%

On the age-curves the points are quite close, and the data would tend to suggest they are contemporaneous. However, the Mascall is Middle Miocene (transitional Hemingfordian-Barstovian) and the San Pablo is Mio-Pliocene (early Clarendonian). The similarities between them are due in large part to the migration factor, as well as to the persistence of relict types under mild climate near the coast.

Altidude.—The method does not provide us with any way to adjust for the important effect of altitude, and hence for the occurrence of "younger" floras in upland areas which lived contemporaneously with the recorded floras of the lowlands. The temperate Arcto-Tertiary Geoflora which occupied lowland areas at higher latitudes in the Early Tertiary, ranged southward in upland areas to mid-latitudes much as present day temperate forests ascend to higher levels at lower latitudes. With cooling climate in the Middle Tertiary, the Arcto-Tertiary Geoflora moved into the lowlands at middle latitudes as the dominant vegetation, displacing the Neotropical-Tertiary Geoflora which had dominated near sites of deposition earlier in the period.

The Green River flora of Colorado and Utah shows how these simple relations are complicated by the graph analysis method proposed by Barghoorn. The Green River plants represented by leaves were chiefly those that lived at or close to the sites of deposition on the lowland basin, and they largely comprise tropical to border tropical genera. But the pollen flora (Wodehouse, 1932; 1933) includes numerous temperate genera of the Arcto-Tertiary Geoflora which lived in the bordering hills where climate was cooler, and they are not represented by megafossils from the site of deposition; similar ecological relations may be seen today in the Sierra Madre of northeastern Mexico. A number of temperate genera represented by pollen are still in the Green River area, but most of those representing the leaf genera are in regions far removed. If we group the figures, the data do not give us a true picture of the age relations, and if we consider them separately, we come up with two ages for the Green River flora.

Reverse relationships existed in the far West in the Late Tertiary, for the lowlands were subhumid owing to desiccation and the uplands now contained "older," more mesic floras which were persisting in favorable, moister sites in the mountains (Axelrod, 1956). A pollen flora containing a mixture of upland and lowland types would thus have a larger number of "exotic" genera and fewer "native" types than a leaf flora from the lowlands. It would thus tend to have a greater age if we follow Barghoorn's thesis.

It is apparent, therefore, that the method does not solve any problem of stratigraphic

correlation where diverse floras are being compared which are represented by pollen as contrasted with leaf, seed, or fruiting material, as Barghoorn believes (1951, p. 743). Since pollen may be transported for long distances from cooler bordering hills to lowland basins of deposition, these upland floras may at one time introduce an element that is "younger" (i.e. Green River, with temperate upland species), and at another time one that is "older" (i.e. Nevada floras, upland forest into the drier lowlands) than the flora at the site of deposition.

Relict environments.—The method does not take into account favorable coastal sites which support relict floras long after they have disappeared elsewhere in the region. Some of the Late Miocene coastal floras of California, such as the Puente, are made up chiefly of the "exotic" group, and would be Early Tertiary if we follow the method proposed by Barghoorn. The subtropical forest that dominated the Puente was persisting near the coast under the influence of mild climate; its elements had a wide distribution in the far West during the Early Tertiary.

Another example is provided by the floras from the Sonoma formation. The Santa Rosa florule lived near the coast (Axelrod, 1944b) but the Napa florulè comes from a site 20 miles farther inland (Axelrod, 1950). The presence of 8 "exotics" at Santa Rosa is consistent with its occurrence in an area where climate was more mild and evaporation lower; by contrast, only 2 "exotics" are recorded at Napa where climate was cooler, and both are hardier types. The comparative figures for the genera in the categories are as follows:

Native: Napa—89%, Santa Rosa—80%
Exotic: Napa—11%, Santa Rosa—20%

On the age-curves drawn by Barghoorn the Napa florule is Late Pliocene, but the florule from Santa Rosa near the coast is Middle Pliocene. Actually, both floras are within a few hundred feet of one another stratigraphically, and both are Late Pliocene (Blancan), and possibly basal Pleistocene if they are high in the Blancan.

Relict environments may occur also in upland areas. The Late Miocene to Early Pliocene floras from the middle to upper slopes of the Sierra Nevada contain numerous "exotic" types, but they are less common in floras from the drier lowlands on the western front of the range. This relationship is demonstrated by the following data for the Carson Pass flora from the Mio-Pliocene summit of the Sierra Nevada, and the Table Mountain flora in the piedmont area:

Carson Pass: native—32%, exotic—68%
Table Mountain: native—50%, exotic—42%, unidentified—8%

On the age-curves proposed by Barghoorn the Table Mountain is Upper Miocene, but the Carson Pass flora is Late Eocene or Early Oligocene; both occur at the base of the same formation.

SUMMARY

For the reasons outlined above, it is apparent that the age-curve method proposed by Barghoorn does not, as he suggests, apply to the floras of a continent, or even to a large part of one. If we consider the method in terms of *local areas only*, it may then be possible to construct curves based on floras whose genera are identified correctly, and use them effectively for age analysis. This was the point of departure for Barghoorn who followed with modifications the method used by Reid for the Late Tertiary floras of northwestern Europe (Reid, 1920). Reid showed there was a marked change in the percentage of "exotic" to "native" species which reflected the relative ages of the Pliocene floras of the region. But the percentages he worked out for that area do not hold for floras in southern Europe (or elsewhere), for the rate of environmental change there differed from that in northwestern Europe, and hence the proportions of "exotic" and "native" types show corresponding differences.

There are no short cuts to determining the age of a Tertiary flora from plant evidence alone. Fossil angiosperms must first be determined correctly in terms of their nearest living counterparts; any flora of moderate to large size with more than 10–15 per cent unknown or unidentified genera is certainly not susceptible to sound analysis (cf. Barghoorn, fig. 3). After the plants have been correctly identified, environment (climate and topography) must then be reconstructed. Only then are we in a position to

evaluate age. This must always be in reference to floras in the *same region*, for those in more distant areas which show relationship are often homotaxial, not synchronous (Chaney, 1936; Chaney & Hu, 1940; Axelrod, 1938). Since Tertiary floras reflect climate, age analysis must of necessity consider the full effects of geographic position and its influence on the composition of vegetation in terms of climate as determined by latitude, altitude, and position with respect to mountains and the ocean. Only by carefully assembling relatively complete successions of fossil floras from many local areas can we hope to arrive at a better understanding of the diverse vegetation types that have migrated widely across this and other continents. With this knowledge in hand, even sounder bases for confidently assigning age on paleobotanical evidence may be developed. The principles that have been used in recent years to determine the ages of Tertiary floras have been discussed in detail elsewhere (Chaney, 1936, 1938, 1942, 1948; Chaney & Hu, 1942; Axelrod, 1938, 1944, 1948, 1956; Dorf, 1942, 1954), and need not be reviewed here.

REFERENCES

AXELROD, D. I., 1938, The stratigraphic significance of a southern element in later Tertiary floras of western America: Jour. Washington Acad. Sci., vol. 28, p. 314–322.

——, 1944a, The Pliocene sequence in central California: Carnegie Inst. Washington Pub. 533, p. 207–224.

——, 1944b, The Sonoma flora (California): Carnegie Inst. Washington Pub. 553, p. 167–206.

——, 1948, Climate and evolution in western North America during Middle Pliocene time: Evol., vol. 2, p. 127–144.

——, 1950, A Sonoma florule from Napa, California: Carnegie Inst. Wash. Pub. 590, p. 23–71.

——, 1956, Mio-Pliocene floras from west-central Nevada: Univ. California Publ. Geol. Sci., vol. 33, in press.

BARGHOORN, E. S., 1951, Age and environment: a survey of North American Tertiary floras in relation to paleoecology: Jour. Paleont., vol. 25, p. 736–744.

——, 1953, Evidence of climatic change in the geologic record of plant life: *in* Climatic Change, p. 235–248, H. Shapley, ed. Harvard Univ. Press.

BROWN, R. W., 1937, Additions to some fossil floras of the western United States: U. S. Geol. Surv. Prof. Paper 186, p. 163–206.

——, 1939, Fossil leaves, fruits and seeds of *Cercidiphyllum:* Jour. Paleont., vol. 13, p. 485–499.

——, 1940, New species and changes of name in some American fossil floras: Jour. Washington Acad. Sci., vol. 30, p. 344–356.

——, 1946, Alterations in some fossil and living floras: Jour. Washington Acad. Sci., vol. 36, p. 344–355.

CHANEY, R. W., 1936, Plant distribution as a guide to age determination: Jour. Washington Acad. Sci., vol. 26, p. 313–324.

——, 1938, Paleoecological interpretations of Cenozoic plants in western North America: Bot. Rev., vol. 4, p. 371–396.

——, 1947, Tertiary centers and migration routes: Ecol. Monogr., vol. 17, p. 139–148.

——, & AXELROD, D. I. (in press), Miocene forests of the Columbia Plateau: Carnegie Inst. Washington Pub.

——, & HU, H. H. (1940), A Miocene flora from Shantung province, China: Carnegie Inst. Washington Pub. 507, pt. II, p. 85–140.

CONDIT, CARLTON, 1938, The San Pablo flora of west-central California: Carnegie Inst. Washington Pub. 476, p. 217–268.

——, 1944, The Table Mountain flora (California): Carnegie Inst. Washington Pub. 553, p. 57–90.

DORF, ERLING, 1942, Upper Cretaceous floras of the Rocky Mountain region: Carnegie Inst. Washington Pub. 508, p. 1–168.

——, 1954, Plants and the geologic time scale: Geol. Soc. Am. Spec. Paper 62, p. 575–592.

MACGINITIE, HARRY D., 1953, Fossil plants of the Florissant beds, Colorado: Carnegie Inst. Washington Pub. 599, 188 p.

REID, E. M., 1920, A comparative review of Pliocene floras, based on the study of fossil seeds: Geol. Soc. London, Quart. Jour., vol. 76 (part 2), p. 145–161.

SCOTT, R. A., 1954, Fossil fruits and seeds from the Eocene Clarno formation of Oregon: Paleontographica, Band 96, Abt. B., p. 66–97.

TRAVERSE, ALFRED, 1955, Pollen analysis of the Brandon lignite of Vermont: U. S. Dept. Interior, Bur. Mines, Rept. Investig. No. 5151. 107 p.

WODEHOUSE, R. P., 1932, Tertiary pollen—I. Pollen of the living representatives of the Green River flora: Bull. Torrey Bot. Club, vol. 59, p. 313–340.

——, 1933, Tertiary pollen—II. The oil shales of the Green River formation: Bull. Torrey Bot. Club, vol. 60, p. 479–524.

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PALEONTOLOGICAL NOTES

ON WALCOTT'S SUPPOSED CAMBRIAN HOLOTHURIANS

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The wonderfully well preserved fossil marine fauna of the Middle Cambrian Burgess shale in western Canada includes a few forms which their discoverer, C. D. Walcott, described as holothurians. His identifications have, however, not been unanimously accepted, although hitherto only one of his species has been definitely referred to another group of animals.

Walcott described four forms in 1911, viz. *Eldonia ludwigi, Laggania cambria, Louisella pedunculata* and *Mackenzia costalis*. In 1918 he described two additional forms, viz. *Redoubtia polypodia* and *Portalia mira*.

H. L. Clark (1912) denied vigorously that any of the forms described in 1911 were holothurians. Of *Eldonia* he says that its general appearance is that of a free-swimming coelenterate, except for the apparently distinct and extraordinary alimentary canal. Of *Laggania* he says that its surface is suggestive of certain worms and actinians but that he does not think it can be positively assigned to any invertebrate phylum. About *Louisella* he remarks that he fails to see why it should be considered a holothurian. *Mackenzia* he thinks suggests certain actinians.

A. H. Clark (1913) supported Walcott's identification of *Eldonia, Laggania* and *Louisella* as holothurians but considered *Mackenzia* an *Edwardsia*-like actinian.

Croneis & McCormack (1939) state that:

> There seems to be little doubt that *Mackenzia costalis* is an actinian . . . , but further information is needed before *Laggania, Louisella* and *Eldonia* can be classified to the satisfaction of all. *Redoubtia* and *Portalia*, . . . , although not certainly holothurians are more convincing as possible Cambrian representatives of the class than the other and better known forms.

The considerable interest attached to the interpretation of any Cambrian fossil, has prompted me to publish also my considerations of Walcott's supposed holothurians.

Mackenzia costalis, Walcott (1911, pl. 13, fig. 2) is undoubtedly correctly interpreted as an actinian; which identification also applies to the specimen figured on pl. 13, fig. 3. In 1918 Walcott (p. 6) adopted also himself that identification of the form.

Eldonia (Walcott 1911, fig. 5) is likewise a coelenterate, a free-swimming form as already suggested by H. L. Clark, viz. a primitive monogastric siphonophore, as I think I have been able to demonstrate convincingly in a paper now in press. The large coiled organ (i) is the gastrozooid, the two clusters (t) gonozooids with gonophores, and the supposed umbrella-shaped body the crown of bracts. Thus *Eldonia* becomes the earliest known representative of the Siphonophora.

Laggania, Louisella and *Redoubtia* I consider all polychaetes, which is nothing sensational, since Walcott described a diversified annelid fauna from the Burgess shale. *Laggania* (Walcott, 1911, pl. 13, fig. 1) and *Louisella* (Walcott, 1911, pl. 13, fig. 4) I regard as sedentary forms, suggestive of the Terebelliformia. The radiating lines on the surface of *Laggania*, easily seen in the figure, are groups of chaeta; the two longitudinal rows of appendages in *Louisella* are parapodia. *Redoubtia* (Walcott, 1918, fig. 5) I consider an errant form, suggesting the Nerediformia.

Portalia (Walcott, 1918, fig. 6–7) suggests superficially a Recent holothurian as, for example, the abyssal *Oneirophanta*, but actually it does not show one single feature which might support such an interpretation. In my opinion it is simply a Porifera of primitive organisation. Its external appearance, the elongate body with the many "appendages" suggests some of the Recent Demospongia. Of inner organisation the fossil shows distinctly a simple tubular cavity with a large osculum at one end.

The find of fossil remains of Holothurioidea in the Middle Cambrian would not be surprising since this group must have diverged very early from the other Eleutherozoa (Echinoidea, Asteroidea and Ophiuroidea) which all are represented at least

in the Ordovician. However, the proof of the existence of a Cambrian holothurian fauna is still lacking, since all the Cambrian forms hitherto recorded as holothurians have been erroneously identified.

REFERENCES

CLARK, A. H., 1913, Cambrian holothurians: Am. Nat., vol. 47, p. 488–507.

CLARK, H. L., 1912, Fossil holothurians: Science, n.s., vol. 35, p. 274–278.

CRONEIS, C., & MCCORMACK, J., 1932, Fossil Holothuroidea: Jour. Paleont., vol. 6, p. 111–148, 4 fig., pl. 15–21.

MADSEN, F. J., 1956, *Eldonia*, a Cambrian siphonophore: Vid. Med. Dansk Nat. For., vol. 118 (in press).

WALCOTT, C. D., 1911, Middle Cambrian holothurians and medusae: Smithsonian Misc. Coll., vol. 57, p. 42–68, pl. 9–13.

——, 1918, Geological explorations in the Canadian Rockies: Smithsonian Misc. Coll., vol. 68, p. 3–20, fig. 2–19.

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ON HEXACTINELLIDA, "HYALOSPONGEA," AND THE CLASSIFICATION OF SILICEOUS SPONGES

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ABSTRACT—Reasons proposed recently in the "Treatise on Invertebrate Paleontology," Part E, for replacing the class name "Hexactinellida" (Phylum Porifera) by "Hyalospongea" are contrary to accepted usage and to the Rules of Nomenclature. The authorship attributed to both names is also erroneous. The "Hyalospongea" of the "Treatise" are not characterised by the accepted diagnostic features of Hexactinellida and include sponges which are not hexactinellid as generally understood. The writer would advocate more emphasis on spicular characters in assessing relationships and discusses their significance in this case. An alternative classification is suggested tentatively.

In the section on sponges of the "Treatise on Invertebrate Paleontology," Part E, M. W. de Laubenfels proposes replacement of the widely accepted class name Hexactinellida by the name Hyalospongea Vosmaer, 1886 (nom. correct. pro Hyalospongiae Vosmaer). As grounds for this he claims (1955, p. 66):

> The name Hexactinellida, which has been used for the class, is inappropriate because spicules other than hexacts are prevalent in some genera and because Hexactinellida is almost identical with the family name Hexactinellidae.

These arguments are open to objection. No valid family name Hexactinellidae exists, nor has the class (or order) Hexactinellida ever been considered distinguished by exclusively hexactinic spiculation.

The taxon usually called Hexactinellida Schmidt, 1870, was originally called Hexactinellidae by Schmidt (1870, p. 13). This name has no generic basis and therefore cannot be used as a family group name. The group was identified as ordinal by Saville Kent (1870) in the same year, and has been accepted generally as an Order/Class group by later writers other than de Laubenfels. The correction of the name to Hexactinellida was made by Carter (1875). Attribution of the group to "Sollas 1887" (de Laubenfels, 1955, p. 66) is puzzling. The name form Hexactinellidae is used invalidly by de Laubenfels for the family whose valid name is Tretodictyidae F. E. Schulze, 1886 (type genus *Tretodictyum* F. E. Schulze, 1886, restr. Ijima, 1927). This family contains the genus *Hexactinella* Carter 1885, but no taxonomic connection can exist between Schmidt's Hexactinellidae and Carter's *Hexactinella*, as de Laubenfels seems to imply (1936, p. 3,185; 1955, p. 78).

In defining his "Hexactinellidae" Schmidt stated (1870, p. 13):

> Ich verstehe unter diese Gruppe alle die jenigen Spongien, deren Kieselnadeln dem dreiaxigen Typus folgen.

As interpreted by Schmidt (ibid.) and later writers, e.g. Carter (1875), von Zittel (1877),

Hinde (1887), F. E. Schulze (1887), Schrammen (1912), or Ijima (1927) among others, this has been regarded as meaning that sponges whose spicules are of basically triaxial type are Hexactinellid irrespective of how many rays individual spicules may happen to have developed as external features. This usage is consistent with Schmidt's diagnosis and has been accepted generally for over eighty years; how it can be "inappropriate" is not clear, unless literally inappropriate is meant.

The two points claimed as grounds for replacing the name Hexactinellida are thus both untenable. In contrast, the consideration that Hexactinellida as generally understood and Hyalospongea as understood in the "Treatise" are not equivalent systematically is not mentioned. Vosmaer's Hyalospongiae was equivalent to Schmidt's Hexactinellidae only; the Hyalospongea of de Laubenfels (1955, p. 66–95) comprise members of the taxa Hexactinellida Schmidt, Heteractinellida Hinde and Octactinellida Hinde together, though this is not shown by the synonymy given (ibid., p. 66).

In defining Hyalospongiae Vosmaer wrote (1887, p. 252):

> Syn. Hexactinellidae Autt. Kieselschwämme, deren Skelet aus isolierten oder gitterförmig verschmolzenen Nadeln besteht. Sämmtlichen Kieselgebilden liegt ein Axenkreuz aus drei einander rechtwinklig schneidenden Centralfäden zu Grunde . . .

Schmidt's Hexactinellida and Vosmaer's Hyalospongiae are thus based on the same systematic concept, namely triaxial spiculation, and are strictly equivalent to one another. Triaxial spiculation is not a characteristic of the Hyalospongea of de Laubenfels (1955, p. 66), nor are all its members hexactinellid. Typical Hexactinellida, including all living and most fossil genera, have spicules with six or fewer rays. De Laubenfels also includes as Hyalospongea other forms with octactinal and polyactinal spicules of types unknown in living Hexactinellida, e.g., *Astraeospongium* F. A. Römer, *Asteractinella* Hinde, in most of which triaxial spicules are wholly unknown. These forms have formerly been placed in separate taxa Octactinellida Hinde and Heteractinellida Hinde by some authors. Their inclusion with Hexactinellida is not justifiable from Schmidt's diagnosis and is neither explained nor pointed out specially under the class heading. Under "Order Heteractinida Hinde" it is stated (de Laubenfels, 1955, p. 93):

> No other sponges have many-rayed siliceous spicules classifiable as megascleres, that is, composing the main body skeleton, although many demosponges and most recent hyalosponges contain polyactinal microscleres.

This comment seems misleading. The only living "hyalosponges" are Hexactinellida, and no known Hexactinellida possess polyactinal microscleres. As is well known, their "astrose" microscleres are astral forms with six or fewer rays; this includes octasters, whose eight pseudoactins do not correspond with the six actinal rudiments at the spicular centre.

The class Hyalospongea of de Laubenfels is thus not based on the spicular character distinctive of Hexactinellida as generally understood, and includes besides Hexactinellida sponges which are not recognisably hexactinellid. Its application to these forms together therefore involves disappearance of Hexactinellida Schmidt not only as a name but as a systematic concept. It seems desirable that this consequence should be made clear; further, caution in accepting it seems justified without better grounds than those cited.

A further taxonomic difficulty arises from the facts that the taxon Hyalospongiae was not originated by Vosmaer but by Claus (1872), and that the relationships of Claus's and Vosmaer's Hyalospongiae to Schmidt's Hexactinellidae as systematic concepts are different. Hyalospongiae Claus, 1872 (p. 153), is defined as comprising sponges:

> Mit zusammenhängenden Kieselgerüsten und geschichteten freie Kieselkorper verkittenden Fasernetzen von Kieselsubstanz, häufig mit Büscheln von langen Kieselhaaren zur Befestigung."

In Schmidt's Hexactinellidae and Vosmaer's Hyalospongiae the basic concept involved is that of triaxial spiculation; this is also the case with the usual alternative name for Hexactinellida, i.e., Triaxonia F. E. Schulze, 1886 (cf. e.g., Schulze, 1887; Schrammen, 1912), which de Laubenfels does not mention. It is not the conceptual basis of Claus's taxon. Further, his Hyalospongiae are not all Hexactinellida; e.g., "*Dactylocalyx*" *pratti*

Bowerbank being a lithistid Demosponge. The introduction of "Hyalospongea" as an alternative to Hexactinellida seems undesirable to the writer for these reasons. It seems possible that de Laubenfels has been misled by Vosmaer's failure to acknowledge Claus as author of Hyalospongiae (cf. Vosmaer, 1887).

If these arguments are followed it becomes necessary to consider an alternative classification of siliceous sponges. The usual basis for classification is the concept of spicular symmetry, accepted by most paleontologists since von Zittel though not used in the "Treatise" account.

In defining Demospongea and "Hyalospongea" in the "Treatise" de Laubenfels makes no use of spiculation (1955, p. 36,66). Many authors have considered two spicular types specially important: the caltrop, a tetraxon with four rays following the axial plan of a tetrahedron, and the hexactin, a triaxon with six rays following the axes of a cube. These have been thought distinctive of spiculiferous Demospongea (=Tetraxonida, Dendy) and Hexactinellida respectively, all spicules of members of each group belonging either to the basic type or others derivable from it (cf. e.g., F. E. Schulze, 1887, p. 496–501). Some Demospongea possess spicules with more than four rays as microscleres, including triaxon-like forms with six rays; not all authors accept these as derived from tetraxons (e.g., Sollas, 1888). However, no known hexactinellid possesses spicules identifiable as tetraxial in origin. In contrast, Demospongiae Sollas, 1885 (seu Demospongea), should comprise sponges lacking triaxons at least as megascleres (Sollas, 1888, p. xcviii).

In paleontology these considerations provide the usual criteria for assessing the relationships of siliceous sponges known from spicular material only. If the two main groups (Demospongea, Hexactinellida) are defined on this basis, it seems reasonable that extinct forms without either tetraxons of caltrop type or triaxons of hexactin type or their recognisable derivatives but having spicules not identifiable as derived from either type should not be included in either of the groups concerned. A small group of Paleozoic genera seems in this category. Hinde (1887) distinguished his Octactinellidae and Heteractinellidae (defined as suborders, not family groups) on similar grounds. These were based on three genera: the former on *Astraeospongium* F. A. Römer, the latter on *Tholiasterella* Hinde and *Asteractinella* Hinde. The spicules of *Astraeospongium*, now type of Astraeospongiidae de Laubenfels, are hexagonal tetraxons, or octactins, with six horizontal rays (three axes) at 60° intervals and two rays (one axis) disposed vertically. This symmetry, though tetraxial, is quite different from that of the tetrahedral type. Other Astraeospongiidae, including *Tholiasterella*, with *Chancelloria* Walcott have comparable spicules with one or both vertical rays lacking, sometimes also with more or fewer horizontal rays (cf. de Laubenfels, 1955, p. 93). *Asteractinella* however has spicules of a different type and belongs elsewhere (Asteractinellidae, de Laubenfels). This small group, excluding *Asteractinella*, appears distinct. Its members typically lack other distinctive spicules. Their grouping as "Hyalospongea" seems to depend on the supposed occurrence of spicules of octactinal type in a hexactinellid, *Hyalostelia* Zittel, placed under Astraeospongiidae. This involves difficulties. *Hyalostelia* was founded on one species, *Hyalonema smithii* Young & Young. The describers' account of this species mentions only pentactine, hexactine and anchorate spicules, i.e. triaxons (1877, p. 426). These were figured together with other spicules; stellate forms were wrongly attributed to *H. smithii* in plate captions though held separate in the text (cf. Young & Young, 1877, p. 430,432; pl. 20). The stellate forms belong to *Tholiasterella*, not to *Hyalostelia* which is a true hexactinellid (Hinde, 1887, p. 109,158,169). Hence Zittel's diagnosis claiming six- and eight-rayed forms together (1879, p. 185) is erroneous; association of hexactinellid and octactinellid spicules, which would imply relationship, cannot be claimed in this case at least.

The genus *Asteractinella* and similar forms (Asteractinellidae, de Laubenfels) seem to comprise a second distinct group. Here the position regarding the spicules is different.

The typical spicules are polyactinal. Hinde found no evidence for their relationship to other types (1887, p. 76–77). However, Weller (1930) has found that *Asteractinella* itself may also have hexactine spicules, i.e., triaxons. On this basis the spiculation might be thought basically triaxial; relationship to Hexactinellida might be postulated, though the typical spicules are not Hexactinellid in Schmidt's sense. The relation of the supposed derivatives to the basic triaxon (i.e., hexactin) would be clearly different from that seen among Hexactinellid spicules, where reduction of rays is typical. The alternative comparison is with demosponge asters, though these are microscleres and not megascleres. It is difficult to regard either comparison as conclusive, though the analogy seems closest in the latter case.

What may be indirect evidence on this problem has recently been found by the writer during studies of the supposed hexactinellid *Spiractinella* Hinde. The six-rayed spicules described by Hinde (1888, p. 164–166) now seem to comprise only some of those actually present. The non-hexactine forms have two, three, four, five or seven rays apart from complications produced by branching. Some of them are conspicuously not of hexactinellid types; in particular the simple forms with three and four rays are triods and caltrops respectively. Such megascleres would normally be attributed to a demosponge without hesitation were the hexactins not also present. It seems more reasonable to interpret *Spiractinella* as a demosponge with megascleres of types now found among microscleres only than as a hexactinellid with spicules of types unknown in any living members of the class. This view is contrary to the diagnosis given by Sollas (1888, p. xcviii; see above); however, this was based on types now living, and it is not surprising to find occasional fossils which do not conform to generalisations on this basis. If this conclusion is accepted, the possibility that Asteractinellidae are also aberrant Demospongea is clearly increased.

At present, however, they seem best regarded as of uncertain affinities and placed in a distinct group; for this the name Heteractinellida can be used in emended sense, basing this on *Asteractinella*. On this basis the sponges with siliceous spicules can be divided into four groups in all. How these should be arranged in classification presents problems; it is difficult to make any arrangement which is not in some way controversial. One simple solution is to regard them as equal divisions of a single class. This is simply a convenient grouping and can be disputed on various grounds; but derivation of several groups separately from a common silica-fixing stock seems at least possible. The name Demospongea (-iae, Sollas) does not fit into this scheme well, but is difficult to replace; the group cannot be characterised by spiculation alone, because it includes keratose sponges and others with no skeleton. Sponges may then be classified as follows:

Class CALCAREA Bowerbank: sponges with skeleton consisting of calcareous spicules.

Class SILICEA Bowerbank (emend. Gray): sponges with skeleton consisting of siliceous spicules, of siliceous spicules and spongin, or of spongin only, or with no spicules.

Subclass Demospongida Sollas: spicules of various types, sometimes lacking; megascleres partly or all tetrahedral tetraxons or their derivatives, monaxons, or desmas, sometimes partly of other types; commonly with spongin and sometimes with spongin skeleton only.

Subclass Heteractinellida Hinde: megascleres astrose, mainly polyactinal but sometimes including six-rayed triaxons; further characters unknown.

Subclass Octactinellida Hinde: megascleres eight-rayed hexagonal tetraxons or comparable forms with more or fewer rays; further characters unknown.

Subclass Hexactinellida Schmidt: spicules six-rayed cubic triaxons or related forms with fewer rays; without spongin.

This proposed classification provides an alternative to that given in the "Treatise," with more emphasis on spicular characters; it can also provide a basis for counter criticism. The class names used can be disputed; for instance, the Calcarea have sometimes been termed Calcispongia (-iae, -ea). Calcarea appears preferable, however, because the alternative seems properly to be a generic name, i.e. *Calcispongia* de Blainville

1830, not an order/class group name as some authors have assumed (cf. e.g., Hinde, 1887, p. 7,85; de Blainville, 1834, p. 530).

REFERENCES

BLAINVILLE, H. M. D. DE, 1834, Manuel d'Actinologie ou de Zoophytologie.

BOWERBANK, J. S., 1862, On the anatomy and physiology of the Spongiadae, parts II and III. Royal Soc. London, Philos. Trans., vol. 152, p. 747, 1087.

CARTER, H. J., 1875, Notes introductory to the study and classification of the Spongida: Ann. Mag. Nat. Hist., ser. 4, vol. 16, p. 1, 126, 167.

CLAUS, C., 1872, Grundzüge der Zoologie.

HINDE, G. J., 1887, 1888, A monograph of the British fossil sponges: Palaeontogr. Soc. Mon., 1887–1912.

IJIMA, I., 1927, The Hexactinellida of the Siboga Expedition: Siboga-Expeditie VI, Leiden.

KENT, W. SAVILLE, 1870, On the "Hexactinellidae" or hexaradiate spiculed siliceous sponges taken in the "Norna" expedition off the coast of Spain and Portugal: Monthly Micr. Jour., vol. 4, p. 241–252.

KIRKPATRICK, R., 1910, On hexactinellid sponge spicules and their names: Ann. Mag. Nat. Hist., ser. 8, vol. 5, p. 208–213.

LAUBENFELS, M. W. DE, 1936, The sponge fauna of the Dry Tortugas: Carnegie Inst., Washington; Pub. 467.

——, 1955, Porifera, *in* Treatise on Invertebrate Paleontology, Part E, p. 21–122.

SCHMIDT, O., 1870, Grundzüge einer Spongienfauna des Atlantischen Gebietes.

SCHRAMMEN, A., 1912, Die Kieselspongien der oberen Kreide von Nordwestdeutschland: II Teil, Triaxonia (Hexactinellida): Paleontographica, Suppt. Bd. 5, p. 177–385.

SCHULZE, F. E., 1887, Report on the Hexactinellida collected by H.M.S. Challenger during the years 1873–1876: Rept. Sci. Res. H.M.S. Challenger, vol. 21.

SOLLAS, W. J., 1888, Report on the Tetractinellida collected by H.M.S. Challenger during the years 1873–1876: Rept. Sci. Res. H.M.S. Challenger, vol. 25.

VOSMAER, G. C. J., 1887, Spongien (Porifera), *in* H. G. Bronn, Thier-reichs, pt. II, Abt. 1.

WELLER, J. M., 1930, Siliceous sponge spicules of Pennsylvanian age from Illinois and Indiana: Jour. Paleont., vol. 4, p. 233–251.

YOUNG, J., & YOUNG, J., 1877, On a Carboniferous *Hyalonema* and other sponges from Ayrshire: Ann. Mag. Nat. Hist., ser. 4, vol. 20, p. 425–432.

ZITTEL, K. A., VON, 1877, Studies on fossil sponges, I, Hexactinellida: Ann. Mag. Nat. Hist., ser. 4, vol. 20, p. 257–273, 405–424, 501–517.

——, 1876–1880, Handbuch der Palaeontologie.

MANUSCRIPT RECEIVED JUNE 14, 1956

NOTICE ON ZOOLOGICAL NOMENCLATURE

Notice is hereby given that the possible use by the International Commission on Zoological Nomenclature of its Plenary Powers is involved in an application relating to the undermentioned name included in Part 9 of Volume 12 of the Bulletin of Zoological Nomenclature, scheduled for publication on September 28, 1956:

Peltura, (emend. of *Peltoura*) Milne Edwards (H.), 1840, validation of (Class Trilobita) [Z.N.(S.)1034].

Any specialist who may desire to comment on the foregoing application is invited to do so in writing to the Secretary to the International Commission (Address: 28 Park Village East, Regent's Park, London, N.W. 1, England) as soon as possible. Every such comment should be clearly marked with the Commission's File Number as given in the present notice.

Extracted from a note from FRANCIS HEMMING, Secretary to the International Commission on Zoological Nomenclature, dated September 20, 1956.

JOURNAL OF PALEONTOLOGY, VOL. 31, NO. 1, P. 287–288, JANUARY 1957

SOCIETY RECORDS AND ACTIVITIES

NEW MEMBERS

In accordance with Article 3, Chapter 1 of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by the Council of the Society.

ALLEN, BILLY DEAN, Room 1, Swallow Hall, Univ. Missouri, Columbia, Missouri: Raymond E. Peck, A. G. UNKLESBAY.

BOWSER, EUGENE OWEN, Dept. Geol., Univ. Kansas, Lawrence, Kansas: M. L. Thompson, Walter Youngquist.

COOGAN, ALAN HALL, Dept. Paleont., Univ. California, Berkeley, California: R. L. Langenheim, Robert M. Kleinpell, R. A. Stirton.

DAVIS, DEL E., 502 South Williams, Denver, Colorado: J. Keith Rigby, Alan B. Shaw.

FOSTER, GLEN LLOYD, 406 Washington St., Galax, Virginia: M. L. Thompson, Walter Youngquist, Richard H. Benson.

GUTENTAG, EDWIN D., 1606 Tennessee St., Lawrence, Kansas: M. L. Thompson, Walter Youngquist, Richard H. Benson.

HEANY, FRANKLIN M., 437 Hamilton Place, Ann Arbor, Michigan: Erwin C. Stumm, Robert V. Kesling, G. M. Ehlers.

HUNT, ALLEN STANDISH, 81 Woodland Ave., New Jersey: Lewis B. Kellum, Erwin C. Stumm.

IVIMEY-COOK, HUGH CHRISTOPHER, Westra Lodge, Dinas Powis, Glamorgan, Great Britain: Robert K. Blundell, H. B. Whittington.

NOBLE, JAMES EUGENE, Room 14, Swallow Hall, Univ. Missouri, Columbia, Missouri: Raymond E. Peck, A. G. Unklesbay.

RODDA, PETER ULISSE, 4052 LaSalle, Apt. 5, Culver City, California: W. P. Popenoe, Daniel I. Axelrod, Alexander Stoyanow.

SALE, HERSHEL EDWARD, 1217 Missouri St., Apt. 2, Houston, Texas: C. M. Quigley, Jr., Paul R. Beach.

SYLVESTER, ROBERT KILBURN, 1506 Del Norte Ave., St. Louis 17, Missouri: Raymond E. Peck, A. G. Unklesbay.

TODD, ROBERT GEORGE, Room 1, Swallow Hall, Univ. Missouri, Columbia, Missouri: A. G. Unklesbay, Raymond E. Peck.

VALENTINE, JAMES WILLIAM, Dept. Geol., Univ. California, Los Angeles 24, California: W. P. Popenoe, Daniel I. Axelrod, Alexander Stoyanow.

VAN SANT, JAN FRANKLIN, Dept. Geol., Univ. Kansas, Lawrence, Kansas: M. L. Thompson, Walter Youngquist.

REPORT OF THE PALEONTOLOGICAL SOCIETY REPRESENTATIVE ON THE NATIONAL RESEARCH COUNCIL, DIVISION OF EARTH SCIENCES, 1956

Matters of interest to members of the Paleontological Society revolve around the status of three committees:

1. Committee on Paleobotany—The committee has been dissolved; no final report has been received.

2. Committee on a Treatise on Marine Ecology and Paleoecology—Proofs of volume 2 (Paleoecology) of the Treatise have been distributed and corrected. Publication of volume 2 is expected this year, and publication of volume 1 (Ecology) early next year. Following publication, the committee expects to be dissolved.

3. Committee on the Measurement of Geologic Time—Since the death of Dr. Marble, this committee has been more or less inactive. Plans for reorganization are still incomplete, but it has been proposed that a reorganized group promote creative work in the field. It has also been proposed that the activities of the committee be expanded to include (1) geochronology, (2) stable isotope distribution with respect to geologic problems, and (3) radioisotope distribution in problems other than geochronology.

Though the Paleontological Society is affiliated with the Division of Earth Sciences, discussions of some importance to us have been held by the Division of Biology and Agriculture. It seems appropriate to call attention to Publication 399 of the National Research Council, "Biological Materials: Part I—Preserved Materials and Museum Collections." This publication is essentially a summary of the functions of museum and study collections, and a survey of the current problems of museums and of systematic biology. Paleontology has roots in both the Earth and Biological Sciences. I feel sure that it would be to the benefit of our Society if steps were taken to work in conjunction with the Division of Biology and

Agriculture of the National Research Council also.

Respectfully submitted,
ELLIS L. YOCHELSON

NOMINATIONS FOR OFFICERS IN THE PALEONTOLOGICAL SOCIETY FOR 1957–1958

In accordance with the provisions of Chapter III, Section 2 of the By-Laws, the Council of the Paleontological Society announces the following nominations for the offices in the Society for 1957–58:

For President: ARTHUR K. MILLER, Iowa City, Iowa

For Vice-President: KENNETH E. CASTER, Cincinnati, Ohio

For Secretary: HARRY B. WHITTINGTON, Cambridge, Mass.

For Treasurer: CLAUDE C. ALBRITTON, JR., Dallas, Texas

For Editor: ROBERT V. KESLING, Ann Arbor, Mich.

In accordance with Chapter III, Section 2 of the By-Laws it is provided that "Any twenty members may forward to the Secretary other nominations for any or all offices. All such nominations reaching the Secretary at least sixty days before the Annual Meeting shall be printed, together with the names of the nominators, as special tickets."

NOTICE TO ALL MEMBERS OF THE PALEONTOLOGICAL SOCIETY

RAISE IN ANNUAL DUES

The Editor's report submitted at the Annual Meeting in Minneapolis on November 1, 1956, reveals the rapid growth that has taken place in the three issues of the *Journal* which we publish. In 1946 these totaled 312 pages; in 1956, 813 pages, a 37 per cent increase in size having taken place in each of the last two volumes. There is now no backlog of manuscripts and the time an author has to wait for publication is at a minimum. A larger *Journal* costs more to publish, however, and, in addition, we have to sustain a 17 per cent increase in printing costs, beginning with the January 1957 issue. The Council considered this matter at its meeting in Minneapolis, and voted to recommend that, if we are to do no more than maintain the *Journal* at its present size, an increase in dues is necessary. It should be remembered that for many years we have received a generous subsidy from the G.S.A. towards cost of publication, and that the *Journal* is not published solely with funds derived from dues. To maintain the *Journal* at approximately its present size on dues alone would require tripling the present assessment.

An increase in dues can be effected only by a change in our by-laws. A majority of the membership must vote for this change for it to become effective. It is proposed, therefore, that the present paragraph 1 of Chapter 4 (Proceedings Volume, Geological Society of America, April 1949, p. 271) be amended to read:

"The annual dues for Members shall be ten (10) dollars, which will include a subscription to the *Journal of Paleontology*. If a member subscribes to the *Journal of Paleontology* through the Society of Economic Paleontologists and Mineralogists, dues shall be two (2) dollars. No person shall be accepted as a member unless the prescribed dues are paid within two months after notification of election. After the first year, annual dues are payable in advance, on or before November first."

It will be noted that, by agreement with the S.E.P.M. Council, it is recommended that the reciprocal dues be raised from one to two dollars. The provision in the last sentence for payment of dues in advance is to permit the Treasurer to take those who have not paid dues off the mailing list for the January issue of the *Journal*.

Two months after this notice has been published members will be balloted by mail, and the ballot will close one month after the mailing date.

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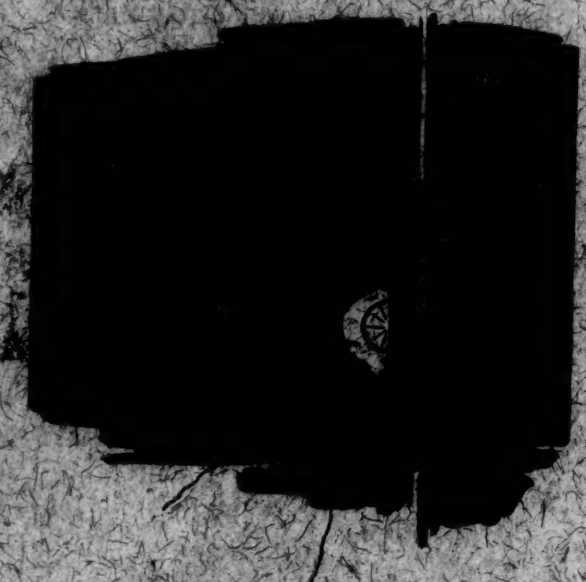

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